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THE MYCORRHIZAL HABIT IN RELATION TO FORESTRY

IV. STUDIES ON MYCORRHIZAL RESPONSE IN *PINUS* AND OTHER CONIFERS

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1. INTRODUCTORY: WAREHAM FOREST, DORSET: A SURVEY.

IN TENSIVE study of an area of poor heathland in south-west England under afforestation has provided exceptional opportunity for observation of the mycorrhizal responses of pines and other conifers to natural soil conditions and to those imposed by experimental soil treatments.

That part of the east Dorset heaths acquired by the Forestry Commission of Great Britain in 1923 and succeeding years, and now known as Wareham Forest, comprises an area of 3,454 acres, of elevation varying from 50 feet to

about 250 feet, lying north-west of the town of Wareham and about 10 miles north of the English Channel. Most of the area was poor *Calluna* heath with a thin covering of 2 to 3 inches of dry heather peat, the vegetation dominated by *Calluna vulgaris* and *Erica cinerea*, with *Erica Tetralix* locally sub-dominant in the wetter parts. *Molinia coerulea*, *Argrostis setacea*, *Ulex nana*, and *Pteridium aquilina* were local constituents, with small *Sphagnum* bogs in the lowest lying parts. The soil was podsolized with much local variation in the character of the layers below the surface peat, as revealed by soil profiles in pit sections. (13).

Sowings of various species of pine in 1926 gave poor and irregular results, a large proportion of the seedlings dying outright or passing into a condition of more or less complete check. It is still possible, 14-16 years after these original sowings, to find surviving seedlings a few inches high. The root systems of such plants from untreated soil, even when quite young, were very defective with intermittent die-back of the younger root tissues, marked deficiency in the number of short roots, and corresponding poverty of mycorrhizas. No evidence of actual root disease or parasitic attack by any soil organism was ever observed, nor was there detected any sign of pseudomycorrhizal association. In the better plants from untreated soil the root symptoms just described were less marked, forked mycorrhizas occurred sparingly, and these showed structural peculiarities now known to be constant and characteristic reactions to local soil conditions.

In 1930 the greater part of the area was tractor-ploughed with obvious benefit to soil drainage and aeration, and marked improvement in the subsequent growth both of pines and of such members of the natural vegetation as reappeared spontaneously. In spite of this many of the failures and inconsistencies of tree growth persisted locally, and evidence of the untoward effects on growth can still be observed in young pines sown or planted in the ploughed area.

At about this time (1930) researches were initiated by one of the writers to investigate the causes of infertility for tree growth in Wareham soil; in particular, to ascertain whether the observed poverty in mycorrhizal development was due to absence of appropriate mycorrhiza-formers for the species or to unknown soil factors that hindered normal mycelial activities. A full account of these researches, with the conclusions reached, and the practical methods adopted successfully to ameliorate the inhibiting soil conditions, has been given in the earlier papers of this series (14, 15, 16, 19). An independent soil investigation has since provided a secure basis for the provisional conclusions on which were based the compost treatments described in the earlier researches (10, 12, 13). It is believed that the soil reactions revealed by this intensive study have wide significance in relation to organic soils; it remains to be learned to what extent they may be applied to the study of cultivated soils and crop treatments in general.

In so far as the conclusions reached in these Wareham researches have direct relation with problems of afforestation, they are bound up with the mycor-

rhizal habit and the recognition of a mycotrophic element in the nutrition of trees. It is, therefore, not unfitting that the present series of papers should conclude with an account of the mycorrhizal responses observed in the course of the work.

It is a fortunate circumstance that these observations have been greatly simplified by the existence of microbiological peculiarities in the soil, in themselves now recognized as the main cause of its infertility for tree growth (13). It is necessary here to refer only briefly to certain conclusions that bear directly on the problems of mycorrhizal association.

1. There is conclusive evidence that Wareham soil contains 'toxic' factors of biological origin that operate as inhibitors to fungal growth.

2. In laboratory culture the inhibiting action has been directly observed upon a number of soil-borne and air-borne fungi, including proved mycorrhiza-formers as well as other soil species that form pseudomycorrhizal associations with tree roots. So far as is known the effects produced are not lethal, but are evidenced as more or less complete inhibition of mycelial growth and of germination of spores. There is evidence of differential susceptibility among the fungal species observed.

3. The condition of biological inertia thus brought about in the soil is manifested in many ways. It leads to the formation of a substrate unfavourable to root growth and affects mycorrhiza-formation directly by inhibiting mycelial activity, although suitable mycelium may be present in the neighbourhood of roots. Reduced fungal activity as compared with that in non-toxic soils of similar type is confirmed by direct microscopic examination; fungus mycelium is relatively scarce and there is a notable absence of the peritrophic fungus flora often conspicuous about roots and mycorrhizas. These characteristics greatly simplify observation of the mycorrhizal relationships in Wareham soil: there are present only few fungal species that form mycorrhizal associations with the roots of pines and other conifers, and there is a notable absence of activity on the part of soil fungi known to cause parasitic or pseudomycorrhizal attack on roots; the task of isolating mycelia of the fungus associates from individual mycorrhizas is thereby made comparatively easy.

2. MYCORRHIZAL RESPONSE IN *PINUS* SPP.

A number of species of pine have been sown or planted at Wareham: Scots pine, Corsican pine, Lodgepole pine, Monterey pine, and Maritime pine. Of these, Maritime pine (*P. Pinaster* Ait.) is the species most resistant to local conditions, and in parts of the area young trees derived from the original sowings are now growing vigorously. Corsican pine (*P. nigra* var. *calabrica*, Schneid.) has proved to be less susceptible than Scots pine (*P. silvestris* L.) both to inhibiting soil factors and to insect attack. Many young trees of the former species planted on the ploughed area are healthy and growing well although inconsistencies of behaviour can be often observed, individual trees becoming chlorotic and going into check in close proximity to others apparently healthy and vigorous. Lodgepole pine (*P. contorta* var. *latifolia* Engel.) and Monterey

pine (*P. radiata* Don.) are both subject to the curious disorder known as 'Fused Needle', and for this reason have been avoided in recent plantings. The account of mycorrhizal behaviour that follows relates to Scots pine and Corsican pine; corresponding observations on Lodgepole pine and Monterey pine by the use of soil inocula brought recently from native stands in California are in progress (see p. 15). Many of the observations that follow are known to apply to Maritime pine, but no special experimental work has been carried out with this species.

Inspection of the experimental area throughout the year with subsequent examination of collected material led to the following general observations.

Mature trees of Scots pine on rather better soil in woods adjoining the area show free development of mycorrhizas in the upper 9 inches of soil. These are of two kinds due to association with *Boletus bovinus* and *Mycelium radicis nigrostrigosum* Hatch, respectively. Sporophores of the former species are abundant in these woods in autumn. On the experimental area sporophores of *B. bovinus* appear in profusion around and within groups of young trees of Maritime pine derived from the original sowings; sporophores have been recorded also under derelict trees of Scots pine (self-sown), and now appear regularly on experimental seed plots and patches of Scots pine and Corsican pine that received compost treatment at the times of sowing in 1933 and 1936. Otherwise, no sporophores of this or other species of *Boletus* have been recorded on the experimental area, although those of *B. elegans* occur in and about larch woods nearby. Other hymenomycete species with sporophores sufficiently conspicuous to have been noted are *Clitocybe (Laccaria) laccata* and *Thelephora terrestris*, both abundant especially towards the boundaries of the experimental area, and *Boletus erythropus*, *B. badius*, *Lactarius rufus*,¹ and *Rhizopogon rufus* immediately outside it.

a. Mycorrhizal Associations

Melin and others had provided a general background of knowledge respecting the identity of a number of mycorrhiza-formers of Scots pine; no information was available as to that of root associates of Corsican pine or of either of the other two species of pine under observation. *Boletus bovinus* is a recorded mycorrhiza-former of *P. Strobus* (2), and our observations at Wareham prove that it is likewise a mycorrhiza-former of Scots pine, Corsican pine, and probably also of Maritime pine in this country. It is not on record whether or not this species of *Boletus* occurs in native pine forests in Corsica.

Boletus bovinus L. In untreated Wareham soil, whether in the field or in pot-cultures, mycorrhizas of one type only have been observed in Scots pine and Corsican pine, namely, those due to association with *B. bovinus*. These are produced very sparingly and irregularly in field controls, and in rather larger numbers in corresponding pot-cultures where they become progressively more abundant with continuous leaching of the soil (19). Proof of the identity of the

¹ *Lactarius rufus* has appeared recently in and about the earlier experimental sowings in some abundance on treated soil.

fungus associate in these mycorrhizas has been provided by isolation of the mycelium from them and comparison of the isolates in pure culture with standard cultures derived from sporophores of *B. bovinus* on the same media. In all respects, rate and manner of growth, colour, morphological details of the hyphae, and growth reactions to various culture media, the colonies derived from sporophores and from mycorrhizas of Scots pine and Corsican pine are identical (Pl. III, fig. 1).

The standard cultures used in the present work came from three independent sources; namely, young sporophores collected within the experimental area October 1934 and October 1938, and a young sporophore from a pure stand of Scots pine in Surrey, September 1935. The strains thus isolated were identical in appearance and behaviour.

Isolations from mycorrhizas of Scots pine and Corsican pine were made as shown in table I.; this can be done without special difficulty during December and January.

TABLE I. *Isolations of Boletus bovinus from individual mycorrhizas of seedlings of Scots pine and Corsican pine growing in the Wareham experimental area and in pot-cultures of transported soil from this area.*

Species of pine.	Isolate.	Source.	Date.	Remarks.
Scots pine	1a	Seed-plot, Wareham experimental area	Dec. 1935	Plot inoculated with humus from good stand (S8 Co)
"	1b	Seed-patch, Wareham experimental area	Dec. 1938	Control, soil untreated (S Co)
"	1c	" "	Dec. 1939	Treated with hopwaste compost at sowing (S C5)
"	1d	Pot-culture with transported soil	Dec. 1935	Control, soil untreated (S Co)
"	1e	" "	Jan. 1937	Soil treated with hopwaste compost at sowing (S C5)
Corsican pine	2a	Seed-plot, Wareham experimental area	Dec. 1935	Plot inoculated with humus from Corsica, treated straw compost C 7 at sowing (L7 C7).
"	2b	" "	Dec. 1938	Control, soil untreated (L Co)
"	2c	Pot-culture with transported soil	Jan. 1937	Soil treated with hopwaste compost at sowing (L C5)

All cultures from these isolations were identical in appearance and behaviour and resembled in all respects those derived from sporophores.

Buller's method of testing identical or related mycelia was successfully applied to the following combinations (see Table I):

<i>B. bovinus</i> (from sporophore)	×	<i>Mycelium radialis</i>	Scots pine (1a)
" (" ")	×	" "	" " (1c)
" (" ")	×	" "	Corsican pine (2a)
" (" ")	×	" "	" " (2c)

In all these combined cultures the constituent hyphae were similar and formed fusions freely. Attempts to induce fruiting in pure culture have been unsuccessful hitherto; experiments are still proceeding.

The characters of *B. bovinus* mycorrhizas as produced by Scots pine are as follows: forked mycorrhizas, borne singly or in clusters, colour pale to golden brown, tending to be paler in colour and to form tuber-mycorrhizas in untreated soil in the field.

As seen in transverse section, the structure of what may be regarded as the normal balanced type of association with *B. bovinus* is illustrated in the photomicrograph reproduced (Pl. II, fig. 1). This structure is described as 'normal' because it is that found in the mycorrhizas of healthy young trees in active growth either immediately outside the experimental area or within it in soil that has received a dressing of compost.

The modifications that appear in the same mycorrhizas in untreated soil are also illustrated (Pl. II, fig. 2). There is more profuse external development of mycelium giving rise to a thicker mantle, often surrounded by a conspicuous zone of loose hyphae. As shown in the photograph, contiguous mantles frequently coalesce to form tuber-mycorrhizas. There is considerable disintegration of the outer cortical tissues of the root, isolated cells becoming embedded within the mantle, the hyphae composing which show a conspicuous exudate of brownish droplets (Pl. II, fig. 2). These mycorrhizas from untreated soil are easily recognizable with a lens: their rather untidy appearance both externally and in section has earned for them the common laboratory designation of the 'messy type'. These structural peculiarities appear in varying degree throughout the experimental area and are undoubtedly correlated with the incidence of certain soil factors. Intermediate stages may be well observed in pot-cultures, in which better growth of the seedlings and structural changes in the mycorrhizas are correlated with the progressive improvement in soil conditions that follows leaching and better aeration. The aberrant features disappear completely in the mycorrhizas formed by young trees growing vigorously in compost-treated soil, and to some extent in those from soil that has received dressings of basic slag or bone meal, both of which also induce improved growth of the trees. The mycorrhizas formed by Corsican pine in association with *B. bovinus* resemble those just described and show similar structural modifications.¹

In both species of pine, control seedlings from untreated soil have root systems dark in colour and very defective in respect to branching of the main roots and development of sub-laterals (short roots). Of the latter a majority are simple and of small diameter, some non-mycorrhizal, others imperfectly mycorrhizal; a few of the latter may fork once, but remain of small diameter; others form small systems of tuber-mycorrhizas enveloped in a conspicuous general sheath of mycelium. All mycorrhizas, whether normal in structure or

¹ Mycorrhizal association of *B. bovinus* with Maritime pine may be inferred although not definitely proved by isolation of mycelium; the condition in Lodgepole pine and Monterey pine has not been fully investigated.

otherwise, are formed by association with *B. bovinus*, identified in the case of each type by isolation of the mycelium and comparative study in pure culture. While, as might be expected, there is variability in detail in roots of control seedlings from different parts of the experimental area, the general type is always the same, differing most markedly from those of seedlings in the same soil treated with composts or with certain phosphatic manures, and from those plants in humus-inoculated and fungus-inoculated plots (Pl. I, figs. 5, 6, 7).

At their first inception the researches at Wareham sought to explain the marked inhibition of mycorrhiza-development in pine. The earlier papers of this series described how this was shown to be due, not to absence of appropriate root fungi, but to soil conditions inhibiting their activity (14). Independent investigation has since confirmed this conclusion, making clear the nature of the factors responsible and providing proof of their inhibitory action on fungal growth in general including mycelial activity of *B. bovinus* (13).

In this soil treatments that remove the inhibitory effects on fungal growth quickly restore fertility. In practice, the most rapid and efficacious means to this end is the application of certain organic composts, the effects of which tend to be self-propagating. The most delicate indicator of improved growth is the mycorrhizal factor: number and incidence of mycorrhizas and the details of their structure. In young pines the restoration of soil fertility is at once registered by increased production of short roots and their immediate conversion to mycorrhizas of normal structure. There is here no trace of the aberrant structural features shown by the corresponding organs in untreated soil.

As already noted, the actual conditions now known to be responsible for infertility in Wareham soil have in themselves greatly simplified the present observations. Since all fungus growth is inhibited in varying degree, absence of mycorrhiza-formation and (or) the lack of balance indicated by aberrant structural features in those formed, is not, as is so frequently the case, commonly accompanied by parasitic attack or pseudomycorrhizal association on the part of other soil fungi.

Knowledge that mycelium of *B. bovinus* is widely distributed throughout the experimental area, although its activity is more or less inhibited, has illuminated certain earlier observations bearing on this matter. For example, it had long been noted that fungal strands or rhizomorphs of pinkish-yellow colour and characteristic structure are profusely distributed in the soil at certain seasons, especially in the neighbourhood of the roots of pine seedlings (Pl. II, fig. 3). Each rhizomorph is a well-developed hyphal strand consisting of a central region formed by one to three hyphae each 4–5 μ in diameter, enclosed by a sheath of more slender hyphae each of 2–3 μ diameter. The average diameter of the whole organ is 60–70 μ . Clamp-connexions have not been observed in the constituent hyphae. Under certain cultural conditions colonies of *B. bovinus* give rise to similar rhizomorphs, and it has recently been proved that those so abundant in natural soil also belong to this fungus. Similar structures of smaller diameter appear in soil cultures.

After many unsuccessful attempts to cultivate rhizomorphs transferred from field soil to synthetic media, the 'germination' of these naturally occurring rhizomorphs was successfully accomplished. Fresh rhizomorphs collected in late March from the experimental area were superficially sterilized by immersion for 10 seconds in 0.1 per cent. HCl, rinsed in sterilized water, and plated on nutrient media. After 5 days' incubation colonies identical with that of *B. bovinus* developed. Careful examination of the soil in the experimental area at the end of March showed that there was then a great abundance of these rhizomorphs; a month later, when root growth of the pine seedlings was just developing, no trace of them could be detected in the same plots. The fact that they were successfully cultivated on synthetic media at the end of March while similar attempts failed during the winter months suggests that the naturally occurring rhizomorphs represent a resistant phase or resting stage and that the resumption of activity coincides with the start of root growth in spring. It would appear that the rhizomorphs represent a resistant phase or resting stage of *B. bovinus* occurring in the field during the winter months and on special culture media when the food material begins to be exhausted. Further observations concerning their occurrence at various seasons are desirable.

Mycelium radialis nigrostrigosum Hatch. This mycorrhiza-former, obviously responsible for the formation of the dark coloured 'D' mycorrhizas recorded by Melin (8), was described by Hatch as a widely distributed mycorrhizal associate of numerous genera of trees and shrubs in Sweden and in U.S.A. (3). It was placed on record for Great Britain in 1937 by one of the authors as a mycorrhiza-former of Scots pine, and has since been observed in this country as a mycorrhizal associate of larch, Douglas fir, Sitka spruce, beech, and oak (15). The characters of the mycelium and structural features of the mycorrhizas formed by it have been fully described by Hatch in the paper cited and need not to be recapitulated here.

In the British Isles it has been observed as a mycorrhiza-former of Scots pine at a number of stations in England, Scotland, and Ireland. It is a common associate of Scots pine in many parts of the New Forest in soils of similar geological history to those at Wareham, and is abundant in woods outside the experimental area at Wareham, but has not been observed within it except in plots treated with soil inocula known to contain it. Once recognized, the characters of the mycelium and those of the mycorrhizas formed by it are readily identified (3). Nothing is known at present of the identity or systematic position of the fungus species to which this mycelium belongs.

b. Pseudomycorrhizal associations

Mycelium radialis atrovirens Melin. Melin isolated and described under this name two forms (α and β) of a soil fungus with brown mycelium not infrequently associated with roots of Scots pine and other conifers (6). The form isolated by him from Scots pine in Sweden, and named *Mycelium radialis atrovirens* α , attacks mycorrhizas and occurs independently as a pseudomycorrhiza-

former. In pure culture it grows readily on the common synthetic media and is easily identified by the characters of the colonies and hyphae and the formation of characteristic sclerotia; it shows little sensitiveness to hydrogen-ion concentration, thereby differing sharply from the typical mycorrhiza-formers.

A soil fungus agreeing in all respects with that observed by Melin in Sweden is present in the soil at Wareham Forest and has come under observation in many other localities. Attack on individual mycorrhizas is marked externally by dark patches sometimes spreading over the whole organ. Pseudomycorrhizas formed by direct association with short roots are unbranched, of much smaller diameter than mycorrhizas, and often slightly beaded owing to irregularities of growth, changing in colour from dark-brown to black with age. As seen in transverse section, a 'net', often irregular in distribution, invades the outer cortex; the enveloping 'mantle' of hyphae, running more or less parallel to the periphery and forming a crusty investment, gives an appearance of constriction to the root tissues. Within the root the cell-walls thicken and become brownish in colour, and in very severe attacks the cells of the outer cortex may be blocked with the characteristic sclerotia of the fungus; all these features are present also in the long roots when attacked (Pl. III, figs. 2, 3; Pl. V, figs. 5, 6).

While undoubtedly deleterious to health and growth, the degree of virulence and capacity for damage of this fungus appear to vary directly with conditions affecting the general health and vigour of the trees, especially in respect to mycorrhiza-development. Marked check to shoot growth with chlorosis and discoloration of the needles become progressively more marked with increasing intensity of the root attack. With abundance of mycorrhizas and slight incidence of the parasite, the effect on growth is insignificant; in conditions unfavourable to mycorrhiza-formation, conversion of the short roots to pseudomycorrhizas by association with *Mycelium radidis atrovirens* may greatly increase and the deleterious effects on growth become correspondingly greater. The mode of action producing this effect requires elucidation. In many cases there is no obvious parasitism by invasion of the root cells, but the 'crusty' investment of both long and short roots must hinder absorption, and the check to normal mycorrhizal development is always considerable and may be practically complete.

It is fortunate that the soil factors that inhibit fungal growth in Wareham soil operate to a greater or less degree in the case of all species that have come under observation there; *M. r. atrovirens* is no exception. Otherwise, feebleness of mycorrhiza-development might be accompanied, as so often elsewhere, by correspondingly severe attack by deleterious soil fungi such as the species now in question. Actually, this does not occur at Wareham; casual mycelium of *M. r. atrovirens* is infrequent in the soil about roots and has not often been observed to attack roots or mycorrhizas of pine.

The form described by Melin under the name *Mycelium radidis atrovirens* β is not known at Wareham, nor has any other soil fungus attacking pine roots come under observation there.

c. Experimental: Soil Treatments

Addition of composts. The mycorrhizal response that follows application of various organic composts to Wareham soil has been recorded and illustrated (16, 19). Application of compost to seed plots at the rate of 10 lb. per square yard is followed during the subsequent season's growth by a profuse development of short roots, all of which become mycorrhizas due to association with *Boletus bovinus*. The abnormalities of structure observed in similar mycorrhizas in untreated soil are absent. The whole root system becomes markedly lighter in colour, golden brown to brown instead of brown to brownish black, and the reactivation of root growth and mycorrhiza-production is accompanied by vigorous shoot development. These effects on growth brought about by addition of compost are accompanied by, and doubtless associated with, changes in the soil which are apparently self-propagating, since they are maintained spontaneously in subsequent growing seasons and are well marked in a second crop of seedlings raised in the same beds 3 years after the original application of compost.

The action of compost in removing soil factors inimical to fungus activity has been discussed elsewhere (13). There is no reason to doubt that the restoration of this activity manifested in laboratory cultures when compost is added to the soil takes place also in the field under natural conditions, or that the profuse development of mycorrhizas by species of pine is one of the ways in which such fungal activation is expressed. The similar results obtained by addition of the same compost sterilized by successive steamings prove that mycorrhizal activity following its application is not related to the introduction of active mycelium with the compost.

The origin and nature of the stimulus to growth manifested as the remarkable impulse to short root development that precedes conversion of these short roots to mycorrhizas remains to some extent a matter of opinion. In view of the identical phenomena that follow humus inoculation and pure culture inoculation of similar seed plots, however, the conclusion appears to be justified that this stimulus to root production is directly related in some manner at present unexplained to the results of fungal activity in the soil. A fuller discussion of this matter will be found in a later section (p. 30).

Humus inoculation. A field experiment designed to test the growth responses of three species of pine to soil treatments with different composts was described in the second paper of this series (16). For two of these species, Scots pine and Corsican pine, the experiment was carried out in duplicate; one series of seed plots treated with composts only, the other simultaneously with composts and inocula of humus soil containing active mycorrhizas and mycorrhiza-formers for the species concerned. In the second series the plots were double-spaced (2 yards apart) to reduce the chance that fungi introduced with the inoculum would spread to neighbouring plots during the period of the experiment. All plots were randomized: compost-treated plots including those of the series inoculated with humus, duplicated; those receiving no compost, whether or

not inoculated, quadruplicated. The inoculum, at the rate of one pint measure per square yard, was applied by inserting a pinch in each of 25 shallow holes distributed over the seed-bed. The humus used for Scots pine was collected from a healthy stand of mature trees of the species in the New Forest and was known to contain mycelium of three potential mycorrhiza-formers: *Boletus bovinus*, *Mycelium radialis nigrostrigosum*, and an unknown hymenomycete. The humus used for seed plots of Corsican pine came from the forest of Aitone, Corsica, and contained mycelium of at least two unidentified mycorrhiza-formers for the species.

These soil-inoculation experiments were designed to elucidate local conditions in respect to the presence or otherwise of mycorrhiza-formers for Scots pine and Corsican pine. When they were planned, the only evidence available was the fact that mycorrhiza-formation was extremely defective, and the observation that the mycorrhizas developed were aberrant in structure.

The nomenclature used to describe treatments was as follows: Scots pine—S; Scots pine + inoculum of Scots humus—S8. Corsican pine—L; Corsican pine + inoculum of Corsican humus—L7. The different composts were numbered C1, C2, &c.; Co indicates that no compost was added. The term control is here used in reference to plots receiving no humus inoculation and no compost treatment. Plots receiving both humus and compost were designed by S8 or L7 with the compost number added; e.g. S8 C1, L7 C6, &c.¹

From the earliest stages of growth plants in all humus-inoculated plots showed greater vigour, sometimes masked in composted plots in which the treatments brought about greatly enhanced growth, but unmistakably evident in those receiving no compost (S8 Co, L7 Co). As might be expected, the stimulus to growth following humus inoculation appeared sporadically in groups of seedlings and spread thence throughout the plots.

Seedlings from control plots (S Co, L Co) and the corresponding humus-inoculated plots (S8 Co, L7 Co) respectively, at all stages of growth show root differences that may be summarized as follows. Control seedlings have a dark-coloured and defective root system, especially in respect to development of short roots. Such mycorrhizas as are formed show a high proportion with the aberrant structure already described, and are easily distinguishable from the normal type by external examination with a hand lens. Both structural types are due to association with *Boletus bovinus*, and this fungus has been isolated from representative examples of each. Cultures of these isolates on synthetic media resemble one another in all respects and are identical with type cultures on the same media derived from sporophore tissues (Pl. III, fig. 1). At Wareham no other mycorrhizal association has been observed in Scots pine

¹ The constitution of the composts mentioned in this paper is as follows: C1, straw chaff + dried blood; C3, Molinia hay + dried blood; C4, 50 per cent. hardwood sawdust + 50 per cent. straw + dried blood; C5, brewery hopwaste + dried blood; C6, 75 per cent. softwood sawdust + 25 per cent. straw + dried blood; C6a, 75 per cent. softwood sawdust + 25 per cent. birch leaves + dried blood; C7, straw chaff + ammonium sulphate. In each case the nitrogen added as dried blood or ammonium sulphate is 1 per cent. of the air-dry weight of the composting material.

from untreated soil whether in the experimental area or in the same soil transported for pot-cultures (see p. 4). In the corresponding humus-inoculated plots mycorrhizas of three kinds have been observed; namely, those due to association with *Boletus bovinus*, *Mycelium radialis nigrostrigosum*, and an unknown hymenomycete. Those due to association with the two last-named fungi are present in relatively small numbers, and it is evident that they cannot be made responsible for the better growth observed in plants in the inoculated beds in so far as this can be attributed to any effect on nutrition due to mycorrhizal activities. Mycorrhizas formed by *B. bovinus* are present in abundance, their incidence being always much greater in humus-inoculated than in control plots. A majority of these mycorrhizas are normal in structure, whereas in control plots most of those present show the structural peculiarities already noted (p. 6) (Pl. II, figs. 1, 2). It is not possible to judge from inspection what proportion of the *B. bovinus* mycorrhizas in inoculated plots is due to the imported strain of this fungus. Since only a very small amount of humus was used per plot and the activation of seedling growth and mycorrhiza-formation tends to spread from localized patches throughout the plots and takes place during the first season, it is probably safe to infer that a large proportion of them are of this origin, and therefore that the mycelium introduced with the inoculum was in a more 'active' state in respect to forming mycorrhizas than was that already present, the vegetative activity of which is known on independent evidence to be more or less severely inhibited (13).

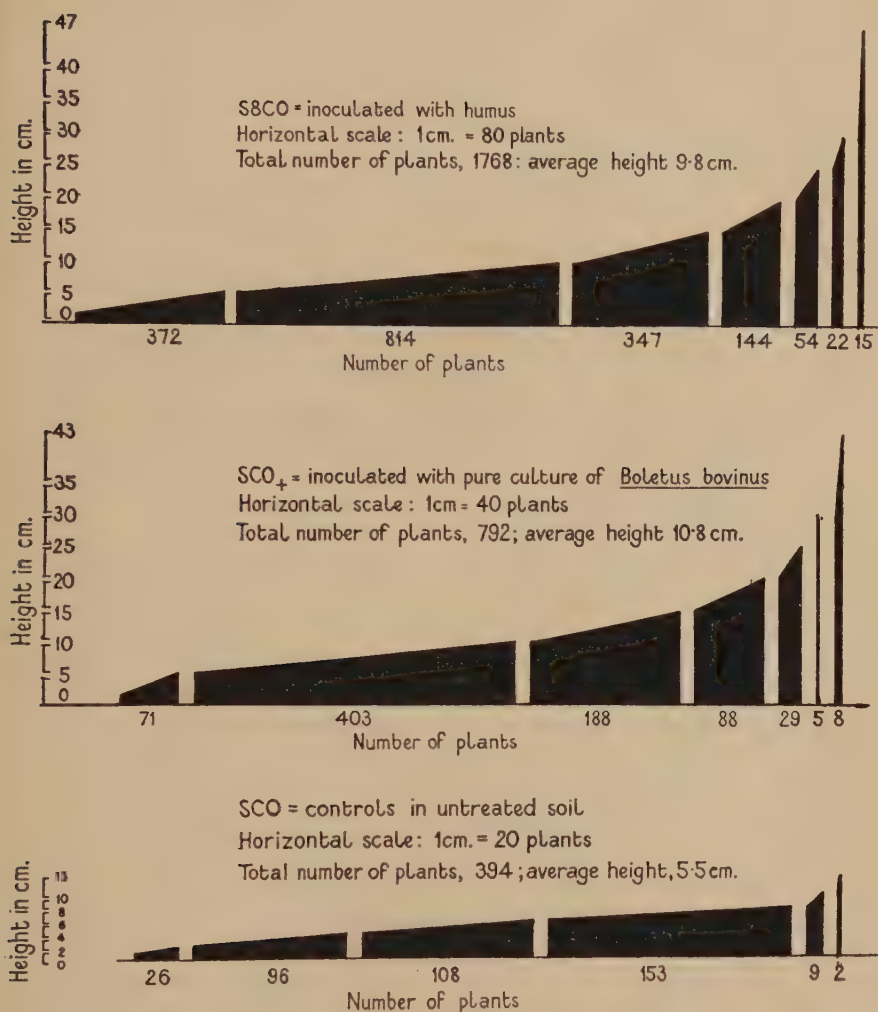
At the time of writing, eight years from sowing, the differences between corresponding plots with and without humus inoculation are very conspicuous, although it can no longer be assumed that the biological effects of inoculation are strictly confined to the former (Pl. I, figs. 1, 3, 4; Pl. IV, fig. 5).

Turning now to plots that received compost in addition to humus inoculation at the time of sowing, it has been noted that differences affecting stature, general habit of the trees, length and longevity of needles, are readily recognizable in the case of certain compost treatments (Pl. IV, figs. 1, 2). In others, e.g. those with composts made from hardwood sawdust that gave negligible or undesirable results in respect to early seedling growth, the effects of humus inoculation added to those of compost treatment apparently tilted the scale in the direction of increased vigour (Pl. IV, figs. 3, 4). The stimulating effect of humus inoculation is not here of a temporary kind; it is still operative nine seasons from sowing and extends unmistakably to resowings after clearance of the first crop.

The comparative heights of plants in control and humus-inoculated plots in the 4th year are shown graphically in Text-fig. 1; the condition of the plots 8 years from sowing is apparent from the photographs selected from a complete record made at this stage.

A pseudomycorrhiza-former was also introduced with the humus inoculum. This is a dark-coloured soil fungus resembling in many respects *Mycelium radialis atrovirens* as described by Melin (6). It has been isolated and is under observation in pure culture. This form of the fungus is probably identical

with that already present and does not flourish in Wareham soil; short roots attacked by it are relatively few in number in control plots and very rare indeed in those that have been treated with compost (see p. 8).



TEXT-FIG. 1. Scots pine. Height-frequency graphs of total populations of three series of seed plots on Wareham experimental area, none of which received compost but two of which were inoculated. The black areas in the graphs represent the number of plants included within the respective height limits indicated in the vertical height scale; the horizontal scale has been varied in accordance with the total population in each series to facilitate comparison.

When these humus-inoculated experiments were carried out, the cause of defective mycorrhiza-development in Wareham soil was still a matter of conjecture and direct inhibition of fungal activity had not been demonstrated.

It is now known that when the latter is relieved, e.g. by compost action, mycorrhizas showing typical structure due to association with *B. bovinus* are formed in relative profusion. Moreover, it has been established with certainty that mycelium of this fungus is present throughout the area, becoming normally active in mycorrhiza-formation with disappearance of the soil factors that inhibit fungal growth. There can be little doubt, therefore, that the poverty of mycorrhizas in untreated soil together with the structural peculiarities exhibited by a majority of those formed, are related directly with the action of these inhibiting factors. Since mycorrhizal activity is much greater in humus-inoculated beds and tends to spread from definite points, it can hardly be doubted that the mycelium of *B. bovinus* introduced with the inoculum is in a condition more favourable to this activity than is the case in that already present. Melin's observations on 'virulence' are of interest in this connexion (6). It must be assumed that the small amount of natural substrate that accompanies the introduced mycelium is sufficient to maintain activity until the renewed vigour in root production and ensuing mycorrhizal development bring about self-propagating soil changes beneficial to growth. It is a matter of considerable interest that the inertia of Wareham soil in respect to fungal activity, with the presence of mycelium of the same mycorrhiza-former both in the untreated native soil and in that introduced as inocula, has made this relatively complete diagnosis possible.

Obviously, it is impossible to evaluate the results of field experiments of this kind with the same strictness as when all conditions are fully controlled. On the other hand, it is equally impossible to refute the striking and uniform character of the experimental results or ignore their significance as a basis for further observations. The conclusions deduced from them in respect to stimulation of growth reinforce those already recorded in this series of papers; they are in agreement with those of Hatch (4) in the U.S.A., and with those of foresters working independently in many parts of the world (18). Their full significance is not easy to assess; yet accurate assessment and full analysis are a prerequisite for any clear understanding of the part played by the mycorrhizal habit in tree nutrition and in soil bionomics in general.

Attention has been drawn to the stimulation of short-root formation that follows seed-bed inoculation with relatively very small quantities of active humus (14). This effect is equally marked in the experiments now under review. Potentially, these short roots are mycorrhizas and become so in due course; but their inception and early development must be independent of any nutritive stimulus associated with or following from mycorrhizal activity (see p. 31).

The Lodgepole pine is among the exotic species subject to the disorder known as fused needle (11, 21, 23) when sown or planted at Wareham. Although it is not yet possible to claim that the failure of short root and mycorrhiza-development observed in the affected plants is causally related to the onset of the symptoms, the fact of such failure is believed to be significant. Since no information was available respecting the identity of mycorrhiza-

formers for this pine in its native habitat, and the condition of the root system of the Wareham plants in respect to mycorrhizal equipment is not regarded as entirely satisfactory, advantage was taken of a visit to California in the spring of 1940 to collect soil from a native stand for use in soil-inoculation experiments. With the kind co-operation of Professor Kotok and his staff at the Forest and Range Experimental Station, University of California, soil containing active roots and mycorrhizas was collected from a pure stand in El Dorado National Forest, California, at the end of March, and used, while still moist, three weeks later, for the inoculation of seed-beds and pot-cultures in this country. The full records and root analysis of these experiments are not yet available; the effect of a small inoculum of the native soil on the early growth of seedlings in pot-cultures is very marked and is recorded in the photographs now reproduced.

For this experiment, 2 series of 12 pots each were sown in Wareham soil. In one, (B), each pot received 5 gm. of the imported soil at the time of sowing; in another, (A), the soil in the pots received no addition; another series (C) was sown in the native Californian soil. Each series was isolated by embedding the pots in clean sterilized shingle in metal containers. The selected pots in each case are fully representative of the plants in the respective series (Pl. VI, fig. 1).

A similar series of experiments with Monterey pine, another species susceptible to fused needle at Wareham, using soil from the native woodlands in the Monterey peninsula, California, are under observation. The results of pot-experiments with this species are not yet available owing to damage from weather during the extremely cold late spring of 1941.

Pure Culture Inoculation. Experimental inoculation of seed plots with sporophore material or with pure cultures of specific mycorrhiza-formers has already yielded results confirming the importance of correct mycorrhizal equipment for pine and other conifers. Thus, in Northern Rhodesia, the use of sporophores of certain hymenomycetes—although not of others—for inoculating seed-beds of *P. longifolia* was followed by favourable growth reactions (18).

At the Forest Research Institute, Buitenzorg, Roelofs (20) made use of pure culture inoculation for seedlings of *P. Merkusii* with markedly beneficial results; it is there reported that *P. Merkusii* is 'completely dependent on the presence of a mycorrhizal infection for normal development' (18). Hatch (4) and Young (22) have also made successful use of pure culture inoculation for promoting the growth of pine seedlings.

In the experimental sowings at Wareham Forest now under survey, certain of the randomized control plots of Scots pine and Corsican pine (S Co, L Co) were inoculated with pure cultures of *Boletus bovinus* 1 year and 2 months after sowing. The inoculations were carried out on similar plots in two experimental areas, one of which was subject to very severe conditions in respect to exposure and in which, for this reason, the seedlings in the selected beds were almost moribund when the treatment was applied. These inoculation experiments were a side issue in the general experimental plan, and the number of plots

available was too small to yield results of critical value. Since, however, these are uniform and in agreement with those obtained elsewhere, and are themselves of interest in respect to certain aspects of mycorrhizal association, they are now placed on record. As the seedlings in one of the experimental areas were already in very poor condition when the treatment was applied, the results obtained in the two areas are recorded separately. In the exposed area all seedlings of Scots pine and Corsican pine in control plots were dead 3 years from sowing; in the two widely separated plots of Scots pine inoculated with *B. bovinus*, one has now a few survivors in fair condition, the other a dense population of vigorous plants. The corresponding plots of Corsican pine both have survivors in fair condition. In the other experimental area the condition of plants in control and certain inoculated plots 6 years from inoculation is shown in the photographs now reproduced (Pl. I, figs. 2, 3; Pl. IV, figs. 5, 6).

It is proposed to repeat these field experiments on a larger scale, testing in the same way the effects produced by using alternatively as inocula pure cultures of another known mycorrhiza-former of Scots pine, namely *B. luteus*. This species of *Boletus* is not known to occur at Wareham, although well known as a mycorrhiza-former of Scots pine in Sweden and widely distributed in pine woods in the northern parts of Great Britain. This matter deserves careful investigation in view of the possibility that the multiple habit of mycorrhizal association in trees is bound up with variation in the stability and efficiency of associations formed by different fungal species in environments varying widely in respect to edaphic and climatic conditions.

Reviewing these results, it is to be observed that the behaviour of seedlings in plots inoculated with pure cultures was similar to that observed in humus-inoculated plots. In both cases, individual seedlings or groups of seedlings of better colour and more vigorous growth appeared sporadically, the growth stimulus tending to spread thence throughout the plots.

The root systems of seedlings in fungus-inoculated plots resemble those of plants from humus-inoculated plots, both differing remarkably from those of plants in control plots in respect to colour, branching, abundance of mycorrhizas, and the comparative absence of aberrant structural features in individual mycorrhizas (Pl. I, figs. 5, 6, 7). The stimulus to growth became effective more slowly in plots inoculated with pure cultures. Whereas in those treated with humus inocula at sowing it was already noticeable in the first season, becoming more marked in successive years, in those subjected to pure culture inoculation in June of the second year, it became conspicuous only several years after treatment. Whether this differential result is related to the different seasons when the inocula were introduced, to the fact that seedlings in the pure-culture treated plots had already suffered from the stringency of control conditions during the greater part of two seasons' growth, or to inherent differences in the activities of the mycelia of *B. bovinus* present in the two kinds of inocula is unknown.

As already noted in experiments with humus inoculation (14), improved

growth in inoculated plots is initiated by marked increase in the number of short roots, all of which are rapidly converted to mycorrhizas.

Accepting the view that nutritional conditions for the seedling are directly associated with mycorrhizal activity, it is evident that the observed impetus towards the production of root initials precedes any possible stimulation due to this cause. The initial stimulus to root production and growth must, therefore, be sought in the surrounding soil. Since it directly coincides with and radiates from points where inocula have been inserted, it must originate in these inocula and is evidently biological in character. Since it is similar in kind when humus is used to that observed to follow inoculation of seed-beds with fragments of natural sporophores or with pure-culture mycelium of mycorrhiza-formers, it is legitimate to infer that the biological constituent concerned in all these cases is mycelium of a fungus or fungi known to form mycorrhizas with the tree species under observation, known to be introduced in the inoculum and observed to be present in the mycorrhizas subsequently developed. The conclusion follows, therefore, that soil activities leading to the stimulation of plant growth are induced by the introduction to seed-beds of suitable inocula, whether of soil, fragments of sporophore tissue, or pure cultures of specific mycorrhiza-formers.

In what does this stimulus consist? In the production of immediately available nutrients in the widest sense, whether by liberation or mobilization of inorganic nutrients from soil constituents by mycelial activity, or production by the same means of simpler from more complex organic materials that can be utilized directly by roots; or is it related directly with the excretion of auxins by the soil mycelia? It appears likely that any or all of these activities may be involved.

The possibilities thus indicated offer a promising field for research; more promising, it is believed, than attempts to evaluate nutritive exchanges in seedlings grown under fully controlled but highly abnormal conditions.

It was hoped to include under the heading of soil treatments an account of the mycorrhizal responses associated with addition of phosphates to the soil of the experimental area. Greatly improved root and shoot growth of pines and other species follows the application of basic slag and bone meal, although not so large or so regular as obtained by use of the more effective composts. Comparative data concerning the permanence or otherwise of the stimulus to mycorrhizal development that accompanies improved growth and the structural reactions as observed in individual mycorrhizas are still incomplete.

3. MYCORRHIZAL RESPONSE IN SITKA SPRUCE (*Picea sitchensis* Carr.).

a. Mycorrhizal Associations; b. Pseudomycorrhizal Associations.

Since little information was available respecting either mycorrhizal-formation, the characters of the mycorrhizas, or the identity of the mycorrhiza-formers in Sitka spruce (5), the details of mycorrhizal development have been studied in material from two native stands in British Columbia and from nurseries and vigorous stands in this country. In general, the more healthy

and thrifty the host tree the more profuse is the development of sub-lateral roots, borne singly or in systems rather less definitely monopodial than those of Norway spruce. Normally, the whole of the short root system is mycorrhizal, the individual mycorrhizas usually clear brown in colour, plump, and of uniform diameter. Lack of vigour in the tree is sharply reflected in the root system by reduction in the number of short roots and decrease of branching, by darkening of colour, and by the smaller diameter of a varying proportion of individual rootlets that taper towards the tip and are often beaded owing to irregularities of growth. The proportion of mycorrhizas present can usually be judged by lens examination: the darker and more slender rootlets may be non-mycorrhizal with root hairs, mycorrhizal with imperfectly developed mantle or other structural irregularities, or mycorrhizal with superimposed attack by *Mycelium radialis atrovirens* or other soil fungi. Invasion of the rootlets and long roots by mycelium of a soil fungus believed to have affinities with *Rhizoctonia* is widespread in British nursery material, and always associated with more or less unthrifty growth.

c. Experimental: Soil Treatments.

Addition of Composts. Attempts to establish Sitka spruce from seed at Wareham gave results extremely discouraging to the forester. The young seedlings, always small, produced shoots about half the normal size with chlorotic and discoloured needles, and a defective root system, dark in colour, with poor development of sub-laterals. Subsequent growth was equally poor and of the same kind. Compost experiments, similar to those described for pine at Wareham, gave a response so encouraging in pot experiments with transported soil that they were extended to field sowings; these gave equally favourable results. The experiments are recorded here in some detail because certain conclusions deduced from them are believed to be of general application to mycorrhizal association in members of the Abietineae, possibly to that in conifers as a whole.

A supply of soil containing roots was obtained from two natural stands in British Columbia, one a mixed stand in Vancouver Island (i), the other, reported as 'a better stand', at Prince Rupert on the mainland (ii). Publication of this paper provides a welcome opportunity to thank the Canadian Forestry Service and their local officers for the collection and dispatch of this material. Both soils were collected in early April and received 3 weeks later, moist, and in good condition; both contained active roots and mycorrhizas of Sitka spruce.

Pot experiments with Wareham soil were duplicated, using a New Forest soil of similar geological origin but without the marked features of infertility that characterize the former. Each set of experiments included three complete series, one receiving compost (C 1, C 5, or C 6 a), the other two the same composts with a 5-gramme inoculum in each pot of one or other of the two Canadian soils. Control series were grown in each of the four experimental soils; other series were included to test the effects of addition of the same composts to the Canadian soils. There were twelve pots in each treatment.

The behaviour of seedlings in the New Forest and two Canadian soils, alone and with additions of one or other of three different composts, is illustrated in part in the photographs now reproduced. Well marked differences of growth were observable between seedlings in the two British soils and the two native soils from British Columbia respectively. Within each group the seedlings showed great uniformity at all stages of growth (Pl. V, fig. 1).

In control plants from these four soils the condition of the roots in respect to mycorrhiza-development is as follows. In Wareham soil rooting is poor in the extremely small seedlings, the root systems deficient in sub-laterals, and very dark in colour. Mycorrhizas of normal structure have not been observed; a majority of the short roots present show imperfect mycorrhizal structure with heavy attacks by *Mycelium radialis atrovirens*, and by another soil fungus with characters resembling those of *Rhizoctonia silvestris* as described by Melin (6), although this fungus has not been observed to attack the roots of pine at Wareham. (Since mycorrhizas of normal structure are freely formed when suitable compost is applied, it may be deduced that a mycorrhiza-former for Sitka spruce is present in the area, a conclusion confirmed by examination of the corresponding plants from field sowings.)

In New Forest soil short roots are produced more freely and mycorrhizas of two kinds are formed due to association with *Mycelium radialis nigrostrigosum* and with an unidentified hymenomycete, yet a relatively high proportion of the rootlets become pseudomycorrhizal owing to attack by a fungus identical in character with *Mycelium radialis atrovirens*. No *Rhizoctonia* attack has been observed in this soil (Pl. V, figs. 3, 4, 5).

In the two Canadian soils seedlings form mycorrhizas with an unknown hymenomycete with hyaline mycelium, also a very small proportion of others by association with *M. r. nigrostrigosum*. Both these mycorrhizal types were noted in the root material included with the soil samples. In both soils the plants suffer attack on the roots by mycelia other than those of the mycorrhizal associates, the heavier taking place in the Vancouver Island soil in which both long and short roots are affected. The identity of the fungi responsible for such attack is discussed later (see p. 20).

In all four soils seedling response to compost treatment resembles that shown by species of pine; marked stimulation of root and shoot growth varying in degree with different composts, and increased production of short roots (sub-laterals) with corresponding mycorrhizal activity and reduction of fungal attack. In New Forest soil, mycorrhizas of two kinds, as described for control plants, are formed freely and the incidence of attack by *M. r. atrovirens* reduced to insignificance (Pl. V, figs. 3, 4).

Humus Inoculation. The following records relate to pot experiments with New Forest soil to which composts alone or composts with inocula of one or other of the two Canadian soils were added.

The immediate reaction to humus inoculation was slight stimulation of growth as compared with that in corresponding pots not inoculated. Towards the end of the first season, and more markedly during the following year, there

became apparent a distinct yellowing of the foliage in plants of all series that received inocula of one or other of the two native soils at sowing. As compared with the corresponding series receiving compost only, there was evidently some loss of vigour resulting in arrest of growth (Pl. V, fig. 2: 1, 11a, 11b), more noticeable in the pots inoculated with Vancouver soil. Yellowing of the foliage appeared also in plants growing as controls in the Canadian soils. The exact significance of this observation was not apparent until the character of the mycorrhizal response in all the series had been studied and analysed. The results of such analyses are now available and may be summarized as follows. Roots and mycorrhizas of plants in all groups receiving inocula of the Canadian soils in addition to composts, and also those of controls in New Forest soil with inocula only, were subject to attack by soil fungi known to be present in the Canadian soils, and observed in the root tissues both of seedlings and of mature trees of Sitka spruce from these soils. Three such fungi have been isolated and studied in pure culture on various synthetic media. They are known only as mycelia, and the following notes respecting their identity are based on careful comparison of their behaviour with that described by Melin for the forms with which they have been identified; in the case of *Mycelium radialis atrovirens* α , also by comparative study with pure cultures of the strains isolated by Melin from Scots pine and Weymouth pine (*P. Strobus* L.) (6).

Mycelium radialis atrovirens α . The form extracted from Sitka spruce resembles in all respects that already described for pine (p. 8). The formation of dark sclerotia in older cultures and very rarely in the outer tissues of attacked roots is characteristic. It is not possible to determine either by inspection of infected roots or by comparative study in pure culture whether the attack by this fungus on the plants in inoculated soil is due to the form already present in New Forest soil or to that introduced with the inoculum. Since attack by the former is observed to be greatly reduced or absent from plants of those groups that receive compost only, it must be inferred that the major part of the relatively light attack on the plants now under discussion is due to the imported strain (Pl. III, fig. 2).

Mycelium radialis atrovirens β . This fungus, as described by Melin (6), differs from the α form in not forming sclerotia in culture and also by bringing about characteristic colour changes in certain media. The strain isolated from Sitka spruce growing in Vancouver Island soil, and in pots that received inocula of this soil, resembles that described by Melin in every respect. It was not observed in the other imported soil (Pl. III, fig. 4).

'*Rhizoctonia*' *sp.* Mycelium of a soil fungus that in pure culture produces characteristic sclerotia, and in other respects resembles that described by Melin as *Rhizoctonia silvestris*, has been isolated from roots of the spruce seedlings growing in both Canadian soils and in all pots receiving inocula of these soils. As a general observation it has been noted that attack by this fungus is intensified by the condition of pot-culture and is not relieved by addition of composts to unfavourable soils as is that of *M. r. atrovirens*. The mycelium invades both long and short roots. In the latter it usually

attacks subsequently to the start of mycorrhiza-formation, causing arrest of the normal development of mantle and net, and itself forming a rather coarse net or pseudotissue between the cells of the outer cortex. In the long roots it forms a characteristic net extending deeply into the cortex without an investing mantle of pseudotissue. In severe attacks and late in the season sclerotia may be formed in the outer cortical cells (Pl. III, figs. 5, 6). In the experimental pot plants now under survey the incidence of this infection is greater in seedlings growing in inoculated New Forest soil with various composts than in those from the native soils. It is relatively severe under pot-culture conditions, and is believed to be the main cause of the yellowing of foliage and deleterious effects on growth observed in the groups of experimental seedlings concerned.

Under recorded conditions, the effect of the root attacks described is not lethal and was least severe in the most vigorous plants. It can, however, hardly be doubted that the observed condition of the root systems in respect to attack by the soil mycelia described was responsible for the yellowing of foliage and appreciable check to growth, or that the fungi in question were introduced with the Canadian soils and could spread from pots inoculated with these soils to others not so treated. Their identity as established in pure culture confirms this view. There is already present in the New Forest soil a form of *M. r. atrovirens* that inhibits normal mycorrhizal development, but the deleterious effects of attack by this fungus practically disappear with addition of composts and subsequent increase of mycorrhizal activity. It is likely, therefore, that any attack observed in plants from groups receiving both composts and inocula is caused by the form introduced with the Canadian soils and not by that present in the New Forest soil. The imported strain of this fungus and of a mycelium with characters resembling that of '*Rhizoctonia*' are thus actively deleterious, causing chlorosis and some arrest of growth in plants from all the composted series. Whether this is due to the greater virulence of the mycelia as such, or to increased intensity of attack in a changed edaphic environment, is an open question. It does not appear to depend on the presence of the form *M. r. atrovirens* β , because the symptoms follow use of either soil, although only one of them is known to contain this fungus. It is believed that the mycelium of '*Rhizoctonia*' type present in both soils is mainly responsible for the deleterious effects observed.

Study of these soil inoculation experiments raises a matter of practical importance in relation to mycorrhizal associations in general. It is already clear that the damage inflicted by soil fungi such as the forms of *M. r. atrovirens* and '*Rhizoctonia*' now under discussion does not depend merely upon the propinquity of mycelium to the roots. Apart from direct effects of the soil environment it is conditioned by other factors such as the vigour of the root system as a whole, the presence of suitable mycorrhiza-formers, and the capacity of the host for mycorrhizal association. In cases where root response is satisfactory in these respects, there appears to be more or less complete immunity from parasitic invasion.

On general grounds it might be expected that indifferent or deleterious fungi of little practical importance under natural conditions where biological equilibrium has been reached might prove to be mischievous when introduced to another soil by operating as a disturbing factor to the equilibrium existing there. The case of Sitka spruce now presented appears to be undoubtedly of this kind. It stresses the need for caution in the empirical use of soil inocula for the purpose of controlling mycorrhizal activities in seed-beds, especially in the case of exotic species and on soils other than those of woodland type. It is evident that some acquaintance with the biological content of the 'humus' so extensively used by foresters as dressings in nurseries is desirable and with the response of the individual fungi concerned to the new environment. Such knowledge can be acquired by laboratory tests and examination, or, as at present, by the often costly method of practical experience. Even when collected with care from a healthy stand of the species for which it is prescribed, it must be noted that every sample of such material is, of necessity, a complex biological system, the ecological balance of which in respect to the roots and the fungal population may be disturbed with change of environment. It is believed that such disturbance is likely to be reflected in the details of mycorrhizal association and is probably the main cause for the inconsistent growth results not infrequently observed to follow such treatments in nursery practice (18).

4. MYCORRHIZAL RESPONSE IN NORWAY SPRUCE (*Picea Abies* Karst.).

Sown or planted in Wareham soil, Norway spruce proved to be even more refractory than Sitka spruce; arrest of root growth and absence of mycorrhiza-development were associated with complete check to shoot growth and severe chlorosis of the foliage. Whether in wet or dry parts of the area, the same symptoms appeared; they were not appreciably relieved by applications of phosphate, whether in the form of basic slag or bone meal, both of which bring about greatly improved growth in other tree species. Observations on the very defective root systems provided no evidence that a suitable mycorrhiza-former was present in the soil. From corresponding observations on *Pinus* spp. it was realized that this negative observation was not in itself of much significance, since it had been already established beyond doubt that the absence or poverty of mycorrhiza-development in species of pine in this area was associated with definite soil factors that inhibit activity of soil mycelia including that of *Boletus bovinus*, a specific mycorrhiza-former, widely distributed and behaving as a typical fungus associate when the inhibiting factors are removed (13).

The observations now recorded were made on sowings of Norway spruce in field plots and pot-cultures subjected to various treatments, inoculated or not with soil from a native woodland near Stockholm. For the collection and dispatch of this material we are indebted to the kindness of Professor E. Melin.

a. Mycorrhizal Associations.

Melin described a number of mycorrhizal associations for Norway spruce in Sweden and identified the fungus associates responsible. Among the latter are

Amanita muscaria, *Cortinarius balteatus*, *Lactarius deliciosus*, probably *Boletus luteus*, and an unidentified mycelium designated as *Mycelium radialis Abietis*, believed to be that of a species of *Boletus* (7). None of the species named are known to occur in the Wareham experimental area. Neither in seed plots in the field nor in the corresponding pot-cultures with transported soil did the puny and chlorotic control seedlings present any evidence that mycelium of a suitable mycorrhiza-former for Norway spruce was present.

b. Pseudomycorrhizal or Deleterious Associations.

Melin has described attack on the roots of Norway spruce by *Mycelium radialis atrovirens*, a fungus known to be present in small amount in Wareham soil where it rarely attacks roots of pine (see p. 12). There was no evidence that this mycelium or any variant of the form associated with pine attacked Norway spruce seedlings, nor that their failure to grow was associated with root attack by any soil fungus.

It was observed that mycelium believed to be that of *M. r. atrovirens* was relatively abundant in the soil sent from Sweden, although no evidence was found that it attacked roots or mycorrhizas growing in this soil. This observation proved to be significant in view of the subsequent behaviour of this mycelium when introduced into Wareham soil.

c. Experimental: Soil Treatments.

Addition of Composts and Humus Inoculation. Experimental work on Norway spruce was carried out in field sowings and in pot-cultures sown in soil transported from the same location. Seed plots were 1 yard square, randomized, treatments duplicated (some quadruplicated), controls quadruplicated. In pot-culture twelve pots were included in each treatment. Both seed plots and pot-experiments included two series, one treated alternatively with one or other of four different composts (C 1, C 5, C 3, C 6a; 10 lb. per plot), or with basic slag (4 oz. per plot), the other receiving the same treatments with addition of an inoculum of the Swedish soil at sowing. The latter was used at the rate of about 1 pint measure distributed in small separate inocula throughout each plot, or 5 grammes per pot inserted below the surface at sowing. The soil in control plots and pots was untreated.

In pot-culture the response evoked by compost treatments was very marked, stimulation of root and shoot growth varying in degree and in rate of action with the compost used. Control seedlings ceased to grow after the first season; the foliage was yellow and the plants moribund or dead 1 year from sowing. In the inoculated series improvement in growth was apparent in the early stages; it was manifested by increased survival value and improved growth in the control plants, and by slight stimulation of growth as compared with those of groups treated with corresponding composts alone (Pl. VI, figs. 2, 3, 4).

Unfortunately, it was not possible to compare the behaviour of plants in inoculated and uninoculated series after the first year, because plants in the

latter were subject to contact infection by fungus growth through the shingle in which pots were plunged. It was observed, however, that plants in the inoculated series all showed slight but progressive yellowing of the foliage with decreased growth during the second year and that these symptoms appeared later in plants of the uninoculated series, spreading from the direction of contact infection from pots inoculated with the introduced soil. This deduction was possible because mycorrhizas identical with those present in the Swedish soil appeared in all pots of the inoculated series and also appeared subsequently in all those of the other series subject to contact infection from them. The fungus associate in these Swedish mycorrhizas has not been identified, and no inquiry as to the mycorrhiza-formers known to be present in the woods whence came the inoculating material can be made at present owing to war conditions. With age, an attack by mycelium of *M. r. atrovirens* became conspicuous in all pots of the inoculated series and spread to those of the other series. The strain of this fungus responsible has been isolated and under pure-culture conditions agrees in all respects with the type cultures of *M. r. atrovirens*.

The field sowings gave results identical with those just described and the slowing down of all growth reactions under field conditions has facilitated their complete analysis. During 2 years all these sowings gave consistently poor growth, their behaviour as compared with corresponding pot-cultures being interpreted as due to the extremely dry conditions that prevailed during the springs and summers of these years. Control plants were very small and extremely chlorotic; they made no growth after the early seedling stage and by the end of the second season were all moribund or dead with the exception of a small group of four or five plants in one plot. As compared with controls, all the compost treatments gave improved growth similar to but less considerable than that in the corresponding pot-cultures. Yellowing of the foliage, entirely absent from pot-cultures receiving compost, was conspicuous in plants of all the seed plots.¹ As in pot-cultures, the introduction of soil inocula conferred survival value in control plots although the survivors were small and chlorotic. No appreciable differences in growth were observable in plants in inoculated and uninoculated plots of the respective treatments in the earlier stages, but those in the former showed increased chlorosis at the end of the second year. The marked slowing down of growth as compared with that of plants in pot-culture was registered in root behaviour not only by decreased branching of short roots but also by arrest of mycorrhiza-formation in those members of the inoculated series receiving soil treatments. At this stage the comparative results of field and pot-experiments were interpreted as indicating that no specific mycorrhiza-former for Norway spruce was present in the experimental soil and that the low rainfall and drought conditions that

¹ The order of effectiveness for compost treatments in pot-cultures was C 5, C 1, C 3, C 6 a; in field sowings C 5, C 1, basic slag, C 3, C 6 a. The constitution of three of these composts has been given in an earlier paper (16); in C 3 a cut of *Molinia coerulea* in late summer replaced straw.

characterize the district operated as a limiting factor to growth of the species, a result already anticipated by foresters.

In the third growing season, an exceptionally dry spring and early summer at Wareham, there was a remarkable change in the behaviour of plants in the field plots. In the uninoculated series the seedlings in all treated plots began to grow, some vigorously, some in less degree according to the treatment given at sowing; chlorosis decreased or disappeared and short roots, often in monopodial systems, were freely produced. Plants in the corresponding groups inoculated with Swedish soil at first showed similar growth reactions, but here growth began to lag towards the middle of the growing season, shorter needles were produced, and chlorosis again became marked. Comparative examination of the root systems in the two series provided the material for complete analysis and confirmed the conclusions tentatively deduced from the corresponding pot plants. A description of the C 5-treated plants will serve as illustration.

Plants from plots treated at sowing with C 5 compost produced few short roots during the first 2 years; those present were slender, unbranched, dark in colour, and non-mycorrhizal. During the third year the impetus to shoot growth observed was accompanied by profuse development of plump rootlets, often associated in monopodial clusters and paler in colour, all mycorrhizal and of normal structure. These mycorrhizas differ from those observed in the Swedish material, and the mycelium present is that of a different fungus associate, the identity of which is still unknown. In these compost-treated plants, no attack by *M. r. atrovirens* was observed and no pseudomycorrhizas were formed.

Plants from the corresponding plots that received both compost and an inoculum of Swedish soil at sowing had root systems of similar type with mycorrhizas like those just described as well as others resembling those formed in Swedish soil and in pot-cultures inoculated with this soil. But many of these mycorrhizas were beaded and dark in colour and showed on microscopic examination all the characteristic features of attack by *M. r. atrovirens*.

As already noted, the control plots contained only one small group of survivors. These showed mycorrhizal development as described for the plants in plots treated with C 5 compost. Control plots that received soil inocula at sowing all had surviving seedlings, but without exception these were small and of poor colour, comparing unfavourably with the few survivors in the uninoculated control plot. Examination of the roots provided explanation of this anomaly, the root systems showing heavy and characteristic attack by *M. r. atrovirens*. The incidence of attack as shown by development of pseudomycorrhizas due to this fungus was notably heavier here than in the plants from plots receiving composts or basic slag without humus inoculation. In general, as proved by root examination, vigour of growth and colour of foliage are related directly with the incidence of attack; as this increases, growth decreases and the needles show more pronounced chlorosis.

The conclusions reached may be summarized as follows:

1. There is a mycorrhiza-former for Norway spruce in the experimental

area at Wareham Forest. The identity of this fungus is still unknown. It is suspected, but not yet proved, that *Boletus bovinus* may function in this way.

2. Mycorrhiza-formation is completely inhibited in the untreated soil and is slow to come into action after treatment with suitable composts (or phosphatic manures). Absence of mycorrhizas has been shown to be directly related with arrested growth and chlorosis in the experimental plants, and is believed to be a main cause of the similar behaviour of Norway spruce plants elsewhere in the area. The extent to which drought is a contributory factor is under investigation.
3. Introduction of another mycorrhiza-former in soil from a native Swedish stand facilitated mycorrhiza-development and promoted growth under pot-culture conditions; but this beneficent action was more than counter-balanced by simultaneous introduction in the same soil of a strain of *M. r. atrovirens*, comparatively innocuous to the welfare of the trees under native conditions, but definitely deleterious when brought into the new environment provided by the soil of the experimental area.
4. These Norway spruce experiments provide, therefore, another example of the risks inherent in the experimental use of soil or humus inocula in tree nurseries without previous attempt to define the conditions present in respect to mycorrhiza-formers or soil fungi known to be deleterious to growth (see p. 22).

5. NOTES ON THE MYCORRHIZAL EQUIPMENT OF LAWSON'S CYPRESS (*Cupressus Lawsonia* Murr.).

This cypress is a native of the northern Pacific States of the United States of America where it occurs as a constituent of woods in moist canyons and similar situations. It is very commonly planted in gardens in this country and is not fastidious in respect to soil or climate under these conditions. So far as is known to the writers, no account of the mycorrhizal relations in this species is on record; it is, however, known that members of the family Cupressineae commonly form endotrophic root associations with a soil fungus belonging to the 'vesicular-arbuscular group of mycorrhizal fungi' (1). The root system of these trees is not, as in pines, spruces, and many members of Cupuliferae, differentiated into long and short roots, the latter normally all mycorrhizas of ectotrophic type.

During the earlier afforestation period at Wareham Forest small experimental plantings of Lawson's cypress were included among those of a number of other conifers. The plants used for this purpose were transplants of nursery origin; one series was planted in untreated soil, in another series each plant received a dressing of basic slag (2 oz.) at planting. When our attention was directed to these trees in 1937, 4 years from planting, they were conspicuous for the vigorous growth made on a very poor light soil frequently subject to drought, and also for the absence of differentiating features in the two sets of plants. Both the control plants and those that had received phosphate were equally healthy and vigorous; in both the foliage was green and there were no symptoms of malnutrition.

This behaviour was so strikingly at variance with that shown by a majority of the other exotic species under trial in the same area and so surprising in view of the natural habitat of Lawson's cypress, that comparative examination of the root systems of the experimental plants, of seedlings from the nursery whence they had come, and of trees growing in a native stand in Oregon, was undertaken. In the Wareham plants 4 years from planting, root infection was identical with that in nursery seedlings of similar origin and with that in root material of indigenous trees from the United States. In plants from all these sources the whole root system including the young active roots proved to be mycorrhizal, showing deep-seated infection by mycelium of a fungus of the vesicular-arbuscular type. The cortical root tissues are traversed by hyphae of large and rather irregular diameter, inter- and intra-cellular in distribution, forming large coils within many of the cells. Typical arbuscular branching was not observed, but large pear-shaped vesicles are abundant at certain stages of growth (Pl. III, fig. 7.). This type of mycorrhizal infection has been fully described elsewhere (1, 19). The characteristic features of root infection are illustrated in the accompanying photographs (Pl. III, fig. 7.).

Pot-experiments with soil transported from the Wareham experimental area were set up under strictly controlled conditions to determine whether the root fungus was present or had been introduced with the transplants. One series of cultures were sown in untreated soil, two others in soil that received additions of basic slag or C 5 compost. Of the resulting plants, the controls in untreated soil were very small with poor root development and discoloured foliage. Addition of basic slag at the rate of 5 grammes or more per pot was deleterious to growth; at the rate of 2 grammes per pot produced no detectable affect. Addition of C 5 compost gave marked improvement of growth comparable with that already observed for pines and other conifers. In none of the experimental plants was any trace of mycorrhizal infection present, an observation since confirmed on plants from another series of pot-experiments and independently from examination of others in field sowings. It must be concluded, therefore, that a fungus species capable of forming endotrophic mycorrhizas exactly resembling those found in this cypress in its native habitat is present in nursery soils and probably in most garden soils in this country. This fungus is not present in the soil of these parts of Wareham Forest where this tree has been sown or planted, and its appearance in plants there was a legacy from the nursery at Oxford where they were raised. Two facts are noteworthy: one that a member of the vesicular-arbuscular group of mycorrhizal fungi capable of forming identical associations with roots of Lawson's cypress is present both in native habitats in the Western United States and in British soils; the other that another member of the same group of fungi present in the mycorrhizas of *Molinia coerulea* throughout the Wareham area does not possess this potentiality.

The sequel to these observations is of some interest. In 1939 it was noted that the cypress plants at Wareham, whether treated with basic slag or not, showed yellowing of the foliage and had ceased to grow. Laboratory examina-

tion proved that mycorrhizal associations had disappeared from roots of the plants treated with basic slag and was present only as traces of fungus infection locally in those of the control plants. It is not yet known whether addition of compost to this soil at planting will bring about change in respect to the persistence of mycorrhizal association in transplants from nursery soils.

Inevitably, these observations point to the conclusions that mycorrhizal association plays a critical part in the nutrition of this conifer and that the ability to form and maintain mycorrhizas is determined by soil conditions. The view still held by some botanists that mycorrhizal association represents a condition of casual parasitism on the part of certain soil fungi is entirely at variance with the evidence yielded by these observations on Lawson's cypress.

6. TECHNIQUE.

The pot-culture experiments described in this paper were made in a special shelter-house of the type used originally by Möller (9). At sowing the pots are embedded in clean shingle, washed, and sterilized with potassium permanganate or formaldehyde solution after each set of experiments. In the second year they are removed to special plunging-pits filled with shingle similarly cleaned and sterilized. In order to avoid contact infection from pots inoculated with pure cultures of fungi or special soils, the following methods have been adopted. The containing walls of all plunging-pits are of concrete treated with several coats of sodium silicate and are divided into separate compartments by similar walls, thus permitting isolation of controls and special soil treatments. The pits are 2 feet deep filled with clean shingle, washed, and sterilized *in situ* by flooding with water or the sterilizing solution, each compartment draining by a separate exit tube near the base into an open concrete-lined drainage ditch. All pots are cleaned and sterilized before use and the embedding material is treated again after removal of each set of pot-experiments. Using these precautions, it has been found possible to maintain freedom from contact infection, and by suitable cultural treatments to grow coniferous and deciduous seedlings in perfect health for 3 and 4 years in London.

For all field experiments subject to inoculation treatments the plots are double spaced, but it is not of course possible to isolate the effects of such treatments indefinitely. In practice, spread of mycelium under field conditions is found to be much slower than that taking place through the moist shingle in which pots are plunged. With randomized arrangement of plots and spacing of at least 2 yards between each plot, perfectly satisfactory results are obtainable for 2 or 3 years from sowing. This is well illustrated in the field experiments with Norway spruce (p. 24).

The technique used for humus inoculation experiments has been described in the text. The need for caution in the use of soil inocula has been stressed in describing experiments with spruces. In order to use such methods to the best advantage in forestry practice, it is desirable to learn something of their content in respect to mycorrhiza-formers and other soil fungi and to ascertain the reactions of these in the soil environment for which they are intended. It

need hardly be added that the material collected for this purpose should be carefully protected from drying-out before use. It should be kept moist and used as soon after collection as possible.

For the isolation and culture of the various root fungi mentioned the ordinary mycological technique has been used with special precautions and culture media as required. Isolations of *Boletus bovinus* from sporophores are best made from young fruit bodies collected during September or October, using the tissue-culture method as follows. Fragments of clean tissue from the inner part of either pileus or stalk of a young fresh sporophore, superficially sterilized, are plated on nutrient agar. Initial platings were made successfully on beer-wort agar or malt agar. The beer-wort agar is prepared as follows: dilute 'sweet wort' as obtained fresh from a brewery to specific gravity 1.04, again dilute to three times the volume with water and add 2 per cent. agar; sterilize by steaming on 2 successive days; do not autoclave. The pH of this medium varies between 4.4 and 5.2. On both beer-wort agar and malt agar so prepared rapid growth of the inoculum takes place in 3 to 5 days forming a raised white colony on the surface of the plate. After 10 to 12 days, the colour changes to pinkish-yellow, the colonies flatten out and develop characteristic zonation (Pl. III, fig. 1). After 3 weeks' growth the hyphae begin to exude staling products and monthly sub-culturing is advisable. The vigour of cultures is maintained by changes of media, among which are used alternatively malt agar, beer-wort agar, and glucose agar. Addition of 0.5 per cent. of a yeast product kindly supplied by Dr. A. C. Thaysen, Department of Scientific and Industrial Research, causes marked stimulation of growth. Even with constant changes of media, pure cultures of *Boletus bovinus* in time lose their characteristic features of vigorous growth, and recourse must be had to fresh isolations. The inocula used experimentally were from pure culture colonies on beer-wort agar or on hopwaste treated with beer-wort, and were prepared by mixing fairly large fragments of the culture media with clean sand; they were inserted just below the soil surface in several places throughout each plot.

7. DISCUSSION.

The case of Wareham Forest is exceptional, because, owing to initial difficulties in afforestation, the soil conditions there have been the subject of unusually intensive investigation, and the peculiarities revealed in the course of the researches provide an especially favourable background against which to view the interaction of mycorrhizal with other fungal activities in soil. This series of papers has already provided independent proof that the mycorrhizal habit plays a significant part in the nutrition of coniferous trees. The evidence leaves no room for doubt in respect to this in so far as the particular soil under investigation is concerned. Lack of correct mycorrhizal equipment is here associated invariably with symptoms of starvation, arrest of growth, and progressive discoloration or chlorosis of the needles—the latter especially in certain species, notably Norway spruce. Mycorrhizal activity, manifested as an annual crop of short roots that become mycorrhizas, whether induced by

soil treatments or by the introduction of specific mycorrhiza-formers as soil inocula or pure cultures, is followed immediately by relief of these symptoms—rapid greening of the foliage and resumption of active growth.

That initiation of mycorrhizal activity in species of pine should follow appropriate soil treatments can be accounted for without difficulty because mycelium of a specific mycorrhiza-former is present in the soil and comes into action with removal of the factors inhibiting fungal growth. Why a similar result should be brought about by the introduction of inocula of a pure culture of the *same* fungus, or of selected humus containing it, is less obvious. Although the mechanism of causation is not apparent, the fact that this occurs is indisputable. The experiments in which a mycorrhiza-former, *Boletus bovinus*, was introduced into field plots either as inocula of a pure culture or in humus were carried out before it had been established that mycelium of this fungus was already present in the soil. Had a different fungal associate been used, the prepotency of the introduced mycelium might be attributable to specific differences. The nature of the observed effects and coincidence of activation with the inoculation centres leave no doubt that the introduced strain of *Boletus bovinus* rather than that already present is responsible for the effects observed. That the inhibiting soil factors operate less effectively in the case of the former is doubtless due in part to the fact that inocula are inserted at a season when the effect of these factors is at a minimum or rapidly decreasing, whereas the mycelium already present has been subjected to their cumulative depressant action with depletion of reserves as a secondary consequence.

The range of variation in growth in control plots that received humus inocula or pure culture inocula at sowing is indicated in the photographs reproduced (Pl. I, figs. 1, 2; Pl. IV, fig. 6). That such variation in response should occur was unexpected, but is not now surprising in view of the known inhibition to fungal growth in Wareham soil and irregularity of distribution in the factors causing it. Should mycorrhizal association be delayed, the introduced mycelium is subject to gradual loss of vigour following exposure to the unfavourable soil environment. It is significant that such irregularity of response to inoculation is a feature of plots otherwise untreated rather than of those receiving composts known to relieve the effects of the inhibiting soil factors.

The increase in root growth and mycorrhizal activity initiated by the introduction of a vigorous fungal strain appears to favour the propagation of improved soil conditions. This is evident from the better growth observable in resowings on humus-inoculated as compared with control plots 3 years after initial treatment, although it is not claimed that the changes thus induced in soil constitution are so fundamental or permanent as those brought about by the more drastic and rapid method of compost additions. The earlier conclusion that 'introduction of active mycorrhizal material into an unfavourable soil leads directly to the production of growth-promoting substances' (14) is reinforced by the observed impetus to short root formation that initiates mycorrhizal activity. Since this follows the use of pure culture inocula, it

must be inferred that the stimulus is in this case associated with activity of a specific mycelium; whether a similar stimulus follows activation of soil mycelium in general cannot be determined under the conditions existing at Wareham, where at least one fungus associate for pines and other conifers is already present, although the necessary conditions for the solution of this problem can now be defined. It is clear that the larger root surface produced will increase the capacity for absorption of water and nutrients and so exert a tonic effect on growth. Of the exact nature of the stimulus to root production nothing is known; the term 'growth-promoting substance' is used in a quite general sense. Nor is it known whether the capacity to bring about such stimulus to root production is limited to those fungal species capable of forming mycorrhizal associations. To the writers it appears improbable that this should be the case. If not so limited, it in no way affects the proven facts that the mycorrhizal relationship in trees forming ectotrophic mycorrhizas is selective in respect to the fungal species concerned, or that absence of the latter from any given soil causes marked disturbance to the growth and health of the trees, often involving attack on the roots by other fungi.

There can be no doubt of the correctness of Melin's conclusion that the mycorrhizal habit is of vital significance (*vitale Bedeutung*) for the plants and trees of organic soils (*Robhumusböden und verwandten Bodentypen*) (6). It is believed, moreover, that the part played in tree nutrition by the mycotrophic habit varies considerably with the soil environment. There is confirmation for this view in observations now on record showing the extreme delicacy with which structural features in mycorrhizas formed by the same associates reflect changes in the surrounding soil, whether arising naturally or brought about by artificial means. The characteristic features of *B. bovinus* mycorrhizas of Scots pine and Corsican pine in Wareham soil and the changes induced by the addition of composts or even by the conditions of pot-culture are examples of this (Pl. II, figs. 1, 2). Structural modifications, equally striking, have been observed to follow additions of different chemical fertilizers to seedlings in adjoining nursery beds. It is legitimate to assume that these changes in structure connote corresponding physiological changes and therefore, alteration of the metabolic relations of root-cells and mycelium. Although conclusive proof for this is lacking it is observed that deviation from the normal in mycorrhizal structure is invariably accompanied by differences in rate of growth, length and colour of the needles, and general health and vigour of the vascular hosts.

There is experimental evidence that the degree of growth stimulation that follows the introduction of a specific mycorrhizal fungus in small inocula of suitable humus depends not only upon the identity of the introduced mycelium but also upon the characters of the treated soil. It is not yet known what is the nature of the determining soil factors or in what manner they operate. It is conjectured that similar factors may come into play in determining the effects of inoculation with pure cultures but there is at present no evidence available in respect to this.

Of great significance also are the changes in resistance to attack by soil fungi

that accompany alteration in the soil environment. Examples of this have been described following the use of inocula of native soils for Sitka spruce and Norway spruce (pp. 18-22).

In Wareham soil a severe attack on the roots of pine seedlings by *M. r. atrovirens*, here normally innocuous, can be induced by the addition of 5 per cent. of pure cellulose to the soil of pot-cultures. In another heath soil of similar type, *Rhizoctonia silvestris* behaves in like manner, producing pseudomycorrhizas encrusted with massive sclerotia on addition of 5 per cent. pure cellulose. In both cases the health of the seedlings suffers severely.

It has been noted that nursery stock of pine seedlings, both in this country and elsewhere, provides frequent examples of abnormality in mycorrhizal structure associated with poor growth. In view of the possibility that this has direct relation with the treatment of nursery soils it is of practical importance that the associated soil conditions should be recognized and defined in as many of these cases as possible.

The views already expressed by one of the writers (17) in respect to the theories of nutrition identified with the names of Frank and Stahl respectively have been strengthened by the observations now recorded. As originally stated, these early theories lack the elasticity required for full interpretation of the facts; in both of them the mycotrophic habit is viewed rather as an isolated phenomenon than as a specialized aspect of one of those cycles of biological activity by which soil fertility is continually renewed. Frank was careful to point out, however, that the breaking down of organic residues by the root fungi of trees might release potassium and other essential nutrients as well as sources of nitrogen. In view of the efficiency of fungi in absorbing mineral salts from very dilute solutions, of their capacity to utilize complex organic substances not directly available to higher plants, breaking these down into chemically simpler forms, and of their propensity to excrete substances that behave as growth stimulants, neither the hypothesis of Frank nor that of Stahl is now an adequate expression of the manifold ways by which fungi—mycorrhizal fungi in particular—may react in the metabolism and growth of the higher plants. The higher efficiency of fungi in salt absorption may well be of critical importance in mobilization of minor elements where any of these is present in concentration near the limits of effectiveness for the vascular host. In Wareham soil it is significant that addition of composts is marked by *sustained* and greatly accelerated tree growth, although this is accompanied by keener competition for soil nutrients owing to the activation of soil mycelia in general. (13). The remarkable quickening of tree growth associated with restoration of mycorrhizal activity and *coinciding with increased mycelial competition* in a soil notably deficient in bases and in inorganic nutrients is a call for renewed research in this direction. Some mobilization of inorganic salts, especially phosphates, must be assumed to take place. Is it possible to relate this directly with the restoration of fungal activity that accompanies that of tree growth?

The view reached is that mycorrhizal association is a highly specialized aspect

of the ecological balance normally maintained between the higher plants and their fungus competitors. The study of mycorrhizal association as an isolated phenomenon may obscure its real significance as an edaphic factor, a liaison aspect of soil bionomics linking the microbiological activities concerned in the maintenance of soil fertility with the nutrition of vascular plants. The specific bacterial and fungal associations exemplified in nodules and mycorrhizas are special cases of a complex ecological system embracing members of the surface vegetation and those of the soil microflora.

The constitution of vegetational units and the progressive and retrogressive changes taking place in them have long engaged the attention of plant ecologists. The significance of edaphic factors such as hydrogen-ion concentration, content of bases, basic ratio, water content, &c., is fully recognized; but the significance of these factors to the constitution of the microflora, and the potentiality of the latter to bring about alterations in the soil environment, appears to have been overlooked or taken for granted.

Since trees are a long-period crop, the task of the forester is essentially to further the maintenance of ecological equilibrium whether in natural woodlands or in those artificial plant communities created by afforestation. In the latter the difficulties may be climatic and beyond his control; where they are edaphic in origin, the ecological conditions existing in natural woodlands provide the most appropriate material for profitable study. The use of organic composts in the Wareham experiments was an attempt to apply this principle by direct modification of the humus constituents in the soil, thereby bringing about changes in the substrate promoting the growth of hymenomycete mycelium, a phase of microbiological activity known to be specially characteristic of woodland soils and believed to be indicative of soil conditions favourable to tree growth.

The present account of mycorrhizal response may be regarded, therefore, as in large part an ecological study of the changes that accompanied this experiment in biological control, having for its object the conversion of an infertile heath soil into a fertile woodland soil.

8. SUMMARY.

1. The paper gives an account of mycorrhizal and pseudomycorrhizal association in a number of conifers, observed during 10 years' intensive study of experimental sowings and plantings in an afforestation area in south-western England. The species receiving special attention are Scots pine, Corsican pine, Lodgepole pine, Sitka spruce, Norway spruce, and Lawson's cypress.

2. One fungus species, *Boletus bovinus*, is mainly responsible for mycorrhiza-formation in pines in the afforestation area. It has been isolated from mycorrhizas of Scots pine and Corsican pine and studied in pure culture on various synthetic media. Another mycorrhiza-former, and certain soil fungi that attack roots and mycorrhizas (forming pseudomycorrhizal associations) have also been isolated and studied in pure culture.

3. Evidence is presented that the establishment and maintenance of correct

mycorrhizal equipment in the conifers named is a formal condition for normal and healthy growth under the soil conditions described.

4. Soil inoculation with mycorrhiza-formers in pure culture or in humus has made evident the delicacy of response in mycorrhizal activities, and the sensitiveness with which mycorrhizal structure reacts to edaphic changes.

5. The bearing of these observations on the mycotrophic habit in trees and their significance in ecological relationships as a whole is discussed.

Some of the experiments described in this paper have been made possible by the use of soil and roots from native stands of the various conifers concerned. For the collection and dispatch of the Swedish material we are greatly indebted to Professor E. Melin of Upsala, for that of Sitka spruce from Canada to local officers of the Canadian Forest Service, and for that of *Cupressus Lawsoniana* to Mr. Thornton T. Munger, of the U.S. Forest Service.

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10. DESCRIPTION OF PLATES.

PLATE I. Fig. 1, Scots pine: seed plot, Wareham experimental area, treated with inoculum of Scots pine humus at sowing. Fig. 2, Scots pine: seed plot, Wareham experimental area, treated with inoculum of *Boletus bovinus* in pure culture 14 months from sowing. Fig. 3, Scots pine: control seed plot, Wareham experimental area, untreated soil. Fig. 4, Corsican pine: seed plot, Wareham experimental area, treated with an inoculum of Corsican humus at sowing (no compost added). All photographs of plots 8 years from sowing and on the same scale. $\times \frac{1}{36}$. Fig. 5, typical sample of roots from Scots pine in control plot, untreated soil (Fig. 3). $\times \frac{1}{4}$. Fig. 6, ditto, from plant in plot treated with Scots humus at sowing (Fig. 1). $\times \frac{1}{4}$. Fig. 7, ditto, from plant in plot treated with pure culture inoculum 14 months from sowing (Fig. 2). $\times \frac{1}{4}$. All roots sampled at time of height assessment (Text-fig. 1), 4 years from sowing.

Fig. 1 represents the largest response to humus inoculation; Fig. 2 the largest response to pure culture inoculation, observed in Scots pine; Fig. 4 the smallest response to humus inoculation in Corsican pine. (Cf. Pl. IV, fig. 5, for control plot, Corsican pine.)

PLATE II. Fig. 1, Transverse section of a *Boletus bovinus* mycorrhiza of Scots pine, from Wareham soil treated with compost. The mycelial mantle, details of Hartig net, and almost continuous tannin layer bounding the outer cortex, are well shown. $\times 220$. Fig. 2, Transverse section of *Boletus bovinus* mycorrhiza of Scots pine, from Wareham soil untreated, showing the 'messy type' of structure. The section shows the massive, loosely woven mantles of contiguous mycorrhizas from a 'tuber' system, and the oily exudate on the constituent hyphae; other details as in Fig. 1. $\times 220$. Inset, detail of mycelium in mantle to show exudate. $\times 512$. The identity of the fungus associate in the mycorrhizas figured was confirmed by isolation and cultivation of the mycelium in each case. Fig. 3, Rhizomorph-like hyphal strands of *Boletus bovinus* from seed plots of Scots pine at Wareham; collected early spring. $\times 240$.

PLATE III. Fig. 1, *Boletus bovinus*: type colony on beer-wort agar, 30 days; isolated from sporophore. Colonies of the isolates from mycorrhizas of Scots pine and Corsican pine of same age are identical in all respects with that shown. Fig. 2, *Mycelium radicus atroviensis* α : from Sitka spruce in New Forest soil; colony on malt agar, 10 days. Natural size. Similar colonies of this fungus isolated by Melin from Scots pine and Weymouth pine, and by us from Norway spruce in Wareham soil are identical in all respects with that shown. Fig. 3, *M. r. atroviensis* α : sclerotia and intercellular net in cortex of short root of Scots pine; artificially induced by addition of cellulose to soil in pot-culture. $\times 400$. Fig. 4, *M. r. atroviensis* β : from Sitka spruce in New Forest soil + C5 + inoculum of Vancouver soil; colony on malt agar, 10 days. Natural size. Fig. 5, '*Rhizoctonia*' sp: from Sitka spruce in Canadian soil (1); colony on malt agar, 10 days. Natural size. The colony figured resembles that of *R. silvestris* from Scots pine as described by Melin and isolated by us from pine seedlings in Oxshott soil. Fig. 6, *Rhizoctonia silvestris*, forming coarse intercellular net in long root of Scots pine seedling in pot-culture. Attack induced

by addition of 5 per cent. cellulose to Oxshott soil. $\times 400$. Fig. 7, Lawson's cypress: longitudinal sections of mycorrhizas from nursery plants showing details of mycelial infection (left), vesicles (right). Latter $\times 300$.

PLATE IV. Fig. 1, Corsican pine: seed plot, Wareham experimental area, treated C1 compost + inoculum of Corsican humus at sowing. Fig. 2, ditto: treated C1 compost only at sowing. Fig. 3, ditto: treated C4 compost + Corsican humus at sowing. Fig. 4, ditto: treated C4 compost only at sowing. Fig. 5 (inset), ditto: control plot, untreated soil. Fig. 6 (inset), ditto: control plot, treated with inoculum of *Boletus bovinus* in pure culture 14 months from sowing. All photographs 8 years from sowing and on the same scale. $\times \frac{1}{30}$. Fig. 6 represents the smallest response to pure culture inoculation observed in Corsican pine.

PLATE V. Fig. 1, Sitka spruce: seedlings in pot-culture. Controls: 1, New Forest soil; 7a, Canadian soil (1); 7b, Canadian soil. (2) $\times \frac{1}{4}$. Fig. 2, ditto: 3, New Forest soil + C5 compost; 11a, New Forest soil + C5 compost + inoculum of Canadian soil (1); 11b, New Forest soil + C5 compost + inoculum of Canadian soil (2). The seedlings in 11a and 11b show chlorosis of foliage, more markedly so in 11a. $\times \frac{1}{4}$. Fig. 3, Sitka spruce, transverse section of mycorrhiza formed by *M. r. nigrostrigosum*; details of mantle and outer cortex. $\times 300$. Fig. 4, ditto: transverse section of mycorrhiza formed by unidentified hymenomycete; details of mantle and outer cortex. $\times 250$. Fig. 5, ditto: transverse section of pseudomycorrhiza formed by *M. r. atrovirens*, either by attack on young rootlet or on very young mycorrhiza, more probably the latter; details of mantle and outer cortex. $\times 350$. Fig. 6, ditto: transverse section of mycorrhiza as Fig. 4 attacked by *M. r. atrovirens*; details of mantle and outer cortex. $\times 400$.

PLATE VI. Fig. 1, Lodgepole pine, seedlings in pot-culture: A, Wareham soil; B, Wareham soil + 5 gm. inoculum of Californian soil; C, soil from El Dorado National Forest, California. All 13 months from sowing. $\times \frac{1}{4}$. Fig. 2, Norway spruce, seedlings in pot-culture: Co, Wareham soil untreated; C1, Wareham soil + C1 compost. 18 months from sowing. $\times \frac{1}{4}$. Fig. 3, ditto: right-hand pot, Wareham soil + 5 gm. inoculum Swedish soil; left-hand pot, Wareham soil + C1 compost + 5 gm. inoculum Swedish soil. 18 months from sowing. $\times \frac{1}{4}$. Fig. 4, ditto: Co (left), Wareham soil untreated; Co (centre), Wareham soil + 5 gm. inoculum of Swedish soil; C5, Wareham soil + C5 compost + 5 gm. inoculum Swedish soil. All 27 months from sowing. $\times \frac{1}{4}$.

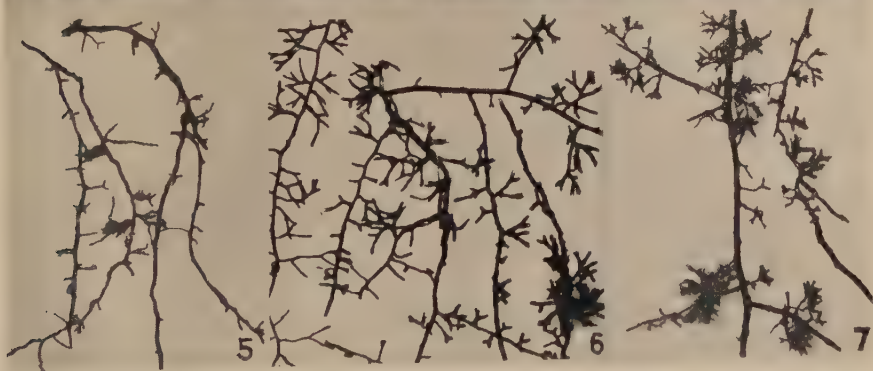
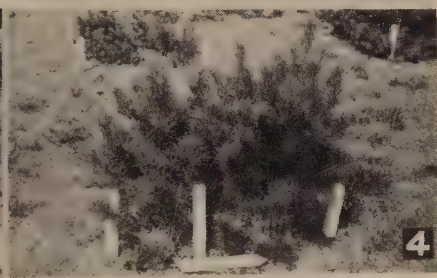
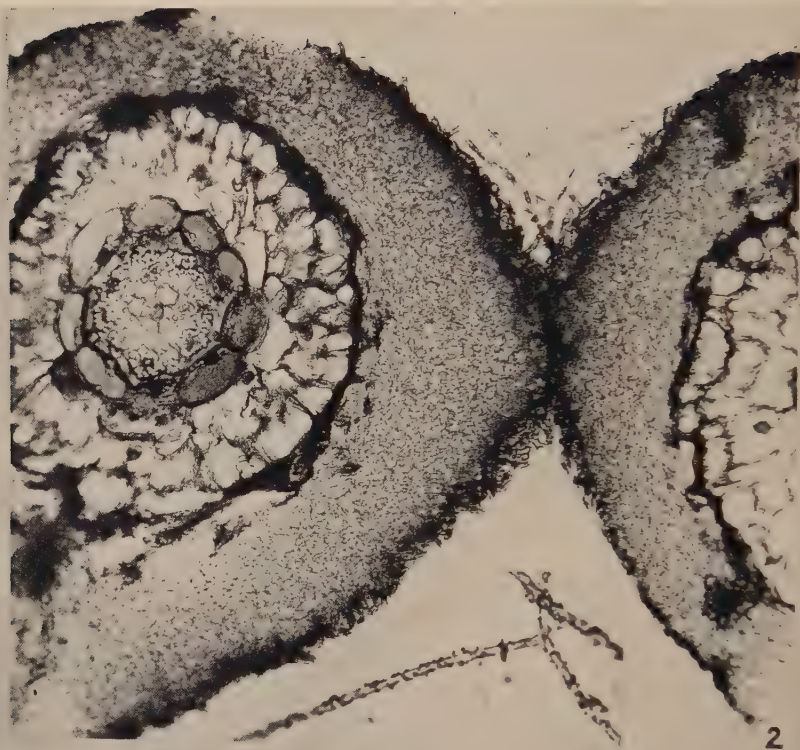
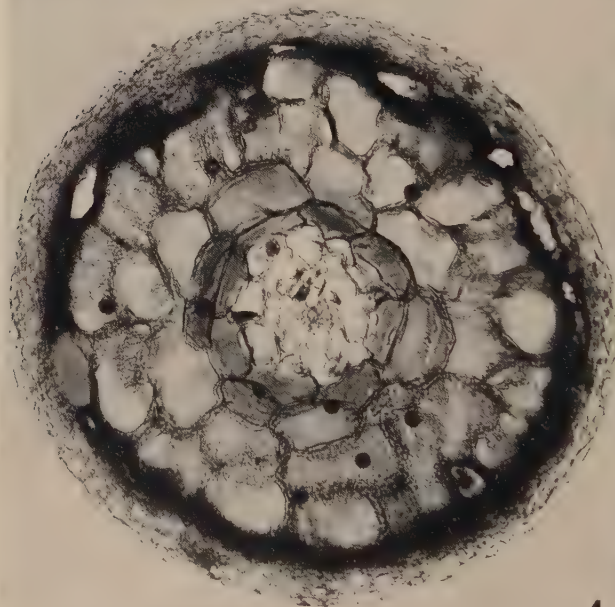


PLATE I



2



1



3

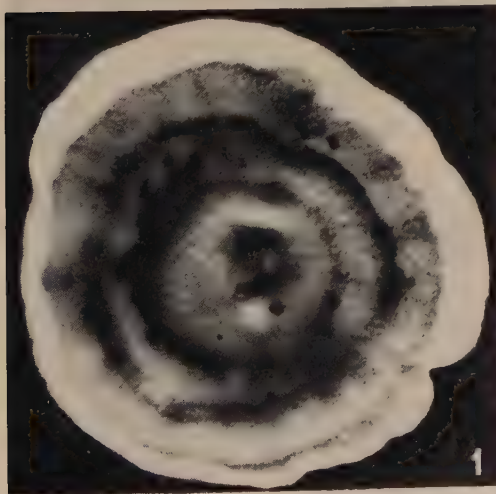
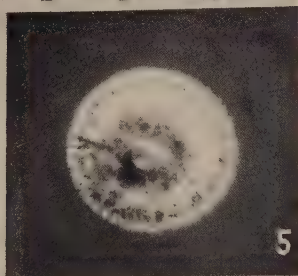
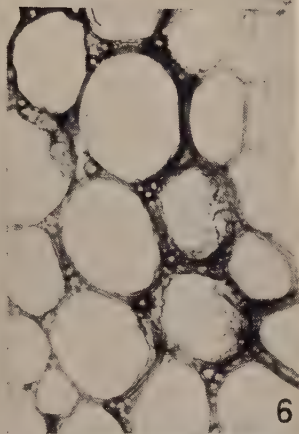
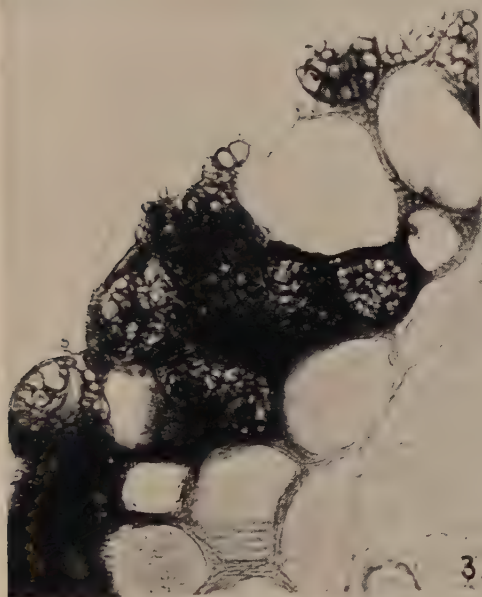
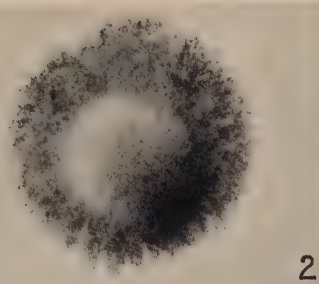
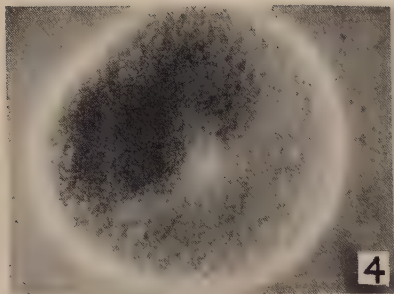
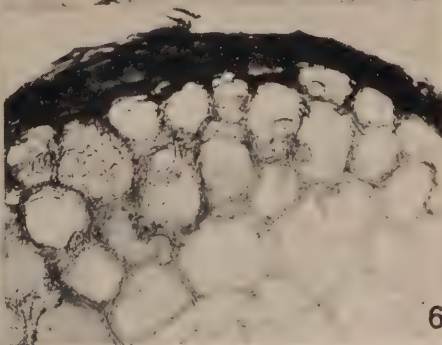
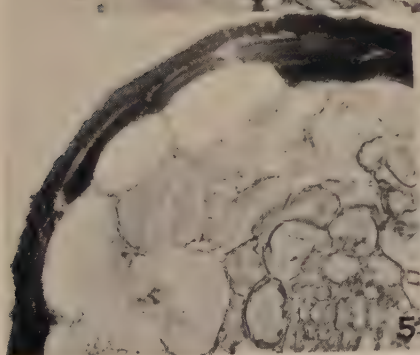
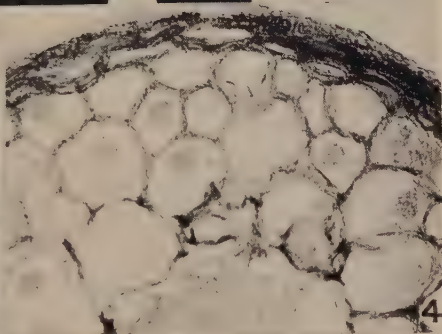
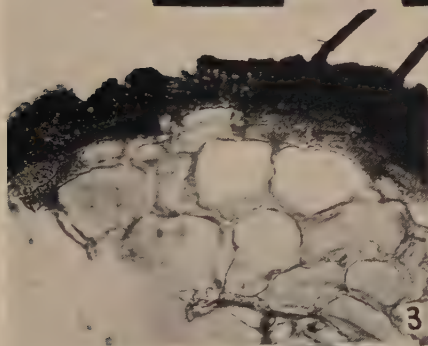
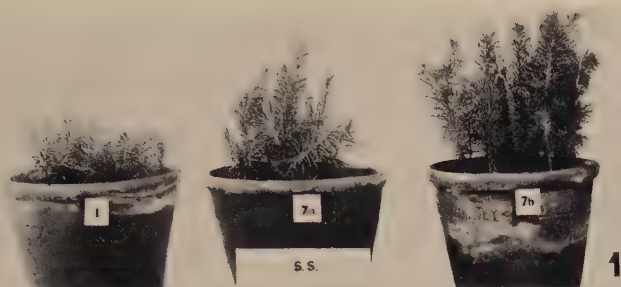


PLATE III



PLATE IV





1



3



C1



C0

2



C0

C0

C5

4

PLATE VI

GLAZED FROST 1940—DAMAGE TO FOREST TREES IN ENGLAND AND WALES

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(*Research Branch, Forestry Commission*)

INTRODUCTION.

TOWARDS the end of January 1940 a most unusual meteorological phenomenon occurred over a considerable area of England and Wales. This was a glazed frost of a peculiar type, exceptional in this country by reason of its wide distribution and the enormous amount of damage caused to trees of all descriptions, to telephone wires, electric cables, and other objects. This paper is concerned particularly with the damage caused to forest trees.

There has been some confusion regarding nomenclature. Certain writers have used the terms 'glazed frost' (10, 20), 'silver thaw' (11, 22, 29), 'rime' (23), and 'ice storm' (6, 8, 9, 12, 14, 15, 18, 19, 26), all with reference to similar phenomena. Other almost synonymous terms are 'frozen rain' (5) and 'ammil' (7), while occasional reference has been made to the French equivalent term 'verglas'. The corresponding German term is 'Glatteis'. The expression 'ice storm' is in frequent use by contemporary writers, but it does not appear to be recognized officially by the Meteorological Office. It is not an appropriate term, as the use of the word 'storm' implies a 'violent atmospheric commotion' (21) which by no means describes the weather conditions prevailing during the phenomenon at present under discussion. It might be as well to quote here the Meteorological Office definitions (21):

'Glazed frost—When rain falls with the air temperature below freezing point, a layer of smooth ice which may attain considerable thickness is formed upon all objects exposed to it. Glazed frost also occurs when a warm damp wind supervenes upon severe cold, the moisture condensing on the still freezing surfaces and thus producing a coating of ice.'

'Silver thaw—An expression of American origin. After a spell of severe frost the sudden setting in of a warm damp wind may lead to the formation of ice on objects which, being still at a low temperature, cause the moisture to freeze upon them and give rise to a "silver thaw".'

'Soft rime—Deposits of white rough ice crystals that grow out to windward on exposed objects when wet fog and frost occur together. The minute supercooled drops of water of the fog freeze when they come in contact with a solid object.'

'Hard rime—Masses of ice deposited chiefly on vertical objects as in "soft rime" but they are formed in "wet air" or supercooled drizzle at temperatures below freezing point and thus have a structure analogous to that of small hail.'

The phenomenon at present under discussion was a true glazed frost, having its origin in the manner described first in the definitions.

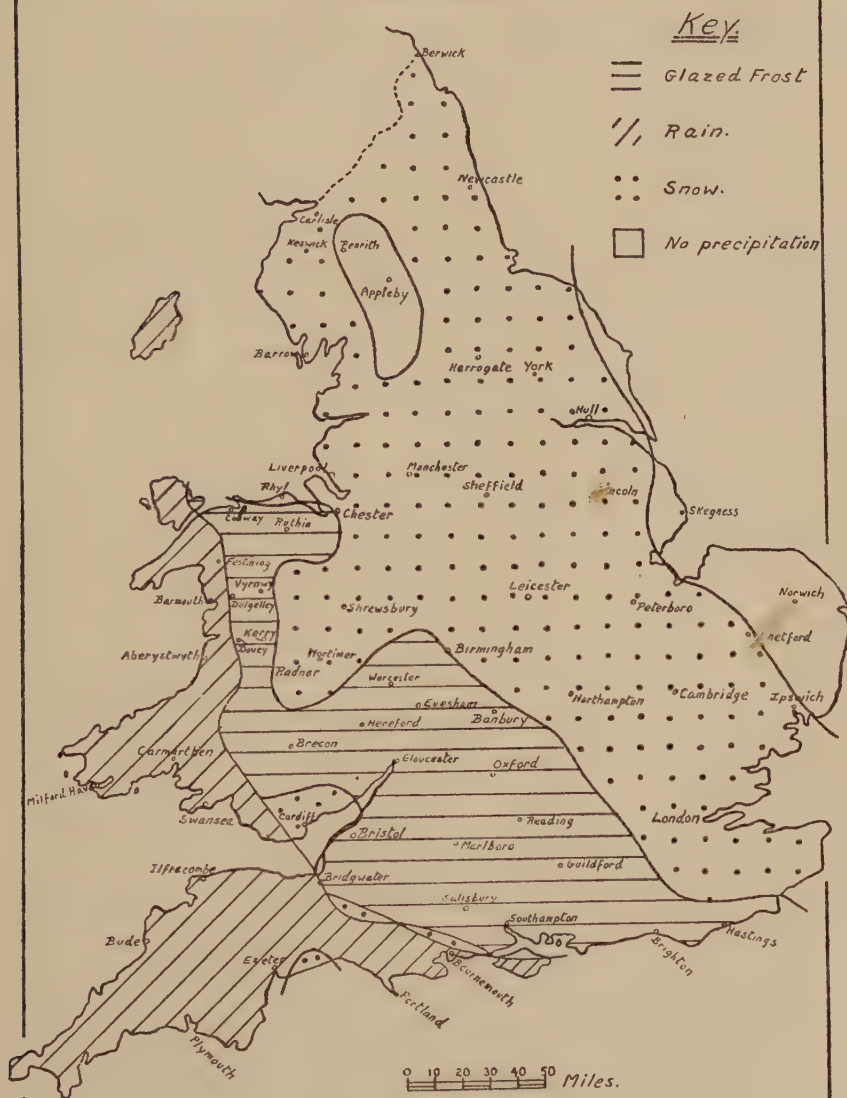
Distribution of the Glazed Frost.January 1940.Note:-

Hachuring indicates approximate distribution of the Glazed Frost including those districts where only high ground was affected.

MAP I

Map showing Precipitation

07
Jan 28th 1940.



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MAP 2

Information has been collected from many sources in the form of reports, published articles, letters, and verbal accounts. The present authors have attempted to summarize these and to augment them with their own observations made some months after the event.

METEOROLOGICAL CONDITIONS.

The weather conditions in various parts of the country leading up to the glazed frost have been described in detail by Mr. C. J. P. Cave (8, 9), and the *Meteorological Magazine* for March 1940 (20) gives a review of the conditions over the whole area affected. It will be sufficient here to give a brief general account.

Following the extremely severe frosts of mid-January, a temporary thaw set in over the south-western half of the country about 25 January. On 27 to 28 January an active but nearly stationary cold front developed in a position running south-east across the English Channel. To the south-west of this front the wind was south-westerly with temperature about 50° F., and there was general rain with no glazed frost. To the north-east the wind was easterly, the temperature below freezing point, and there was either snow or no precipitation. On the north-eastern edge of the front a marked inversion of temperature must have existed with the result that over that part of the country covered by the cold front, rain, falling from the warm upper layer, was cooled to below freezing point in the underlying cold belt without actually solidifying. This supercooled rain froze on all solid surfaces. In some districts it appears to have frozen immediately on striking any solid object, but in other places the water spread over the surfaces before turning into ice.

The frost moved very slowly south-westwards from the Severn estuary to the Scilly Isles, and the glazed frost followed in its wake. In some districts mist occurred after the glazed frost proper and gave rise to the formation of rime in addition to the actual ice layer (20).

DISTRIBUTION.

The area most severely affected by the glazed frost lay to the south-west of a line drawn from Rhyl through Shrewsbury and Banbury down to Hastings. The counties covered by this belt of heaviest ice deposit were: Merionethshire, Denbighshire, Montgomeryshire, Radnorshire, Shropshire, Herefordshire, Brecknockshire, Monmouthshire, Worcestershire, Gloucestershire, Warwickshire, Berkshire, Wiltshire, and Hampshire. Parts of Caernarvonshire, Glamorgan, Carmarthenshire, Oxfordshire, Somerset, Dorset, and Devonshire were also fairly severely affected, particularly on high ground. Glazed frost was also recorded from places in Cambridgeshire, Hertfordshire, Essex, Middlesex, Surrey, Sussex, Staffordshire, Nottinghamshire, Lincolnshire, West Riding of Yorkshire, and Derbyshire, but in all these counties the ice deposit was comparatively very slight and damage to forests negligible.

The distribution zone of the glazed frost extended into northern France. The area most severely affected here appears to have been in the Department

of the Seine-Inférieure, especially the open arable country north of the Seine in the region of Yvetot. Here it is reported that miles of telephone poles were snapped off at ground-level and that Scots pine in the forests west and south of Rouen were heavily damaged (12).

ICE COATING.

The thickness of the ice coating was dependent on the combined conditions of temperature and rainfall. As a general rule, the thickness increased with elevation up to at least the 1,800 foot contour, but in certain very exposed areas wind force prevented the maximum deposit forming on the leaders and highest branches of trees, because much of the rain was blown off and fell on to the lower branches before it became ice.

The position of the ice upon twigs, branches, wires, &c., depended mainly on (a) temperature, and (b) wind force and direction. In the colder places, where the rain was appreciably below freezing-point, almost all the ice was on the top of horizontal twigs or wires and on the windward side of vertical surfaces, with little or no icicle formation. Under slightly warmer conditions the ice was mainly on the lower side of horizontal objects with a considerable amount of icicle formation, while on vertical twigs, &c., the ice cylinders were almost symmetrically disposed.

There is a large amount of data available dealing with the thickness of the ice coating in various districts, but it is very difficult to compare these figures, partly due to the personal factor but mainly for two other reasons:

- (i) Some observers have given average measurements, while others have only recorded maximum or range figures.
- (ii) In some districts rime formation occurred after the true glazed frost, and several of the measurements recorded included this secondary deposit as well as the true ice layer.

Post Office reports (24) show that particularly thick deposits occurred in the Worcester-Evesham district, where the ice on telephone wires was often 3-4 inches in diameter and occasionally 7-8½ inches across the longer axes of oval-shaped deposits, these latter weighing up to 3 lb. per foot of wire. It is probable that a large part of these exceptionally thick deposits was actually rime and not solid ice. Twigs in the same district often carried ice cylinders up to 4 inches in diameter, with a weight ratio, before and after thawing, of 64 to 1. As a general rule, however, it was on the higher ground that the heaviest coating was formed, and both Forest and Post Office reports agree that the mountains of central and north Wales, the Mendips, the Cotswolds, Salisbury Plain, and Marlborough were all districts of very heavy ice deposit. The general ice coating on twigs and branches at Kerry Forest was 4 inches thick; in Radnor and Mortimer Forests, 3-4 inches; in the Cotswolds and on Salisbury Plain it was also 3-4 inches, while at Marlborough and in Savernake Forest the thickness was 1-3 inches according to elevation. It seems safe to say that over most of the area severely affected the ice coating averaged approximately 1 inch below the 500 foot contour, 2-3 inches from 500 to 1,000 feet, and 3-4 inches

from 1,000 to 1,600 feet. The Worcester-Evesham district appears to have been a notable exception and to have had a much greater deposit than most districts at similar elevation, but, as stated above, a large part of the coating was probably rime and not solid ice.

RELATIVE DAMAGE TO VARIOUS TREE SPECIES.

When considering the relative ice damage to different species, the following points must be borne in mind:

- (i) The planting sites chosen vary greatly according to species, and those trees normally planted at low elevations cannot be fairly compared with others on high and exposed ground.
- (ii) Age and size of crop are very important factors.
- (iii) Normal forest plantations of one species should not be compared with widely spaced or isolated trees of another variety.

Summarizing the results in all districts, with these points in mind, the following notes indicate the form and intensity of damage to trees under various classifications.

1. *Isolated or very widely spaced Middle-aged or Mature Trees.*

Poplars showed the most severe damage, being often reduced to a single decapitated stem with only the short broken remains of the branches from top to bottom. This is the more remarkable because this species almost always occurs at low elevations where the ice deposit was usually only moderately thick. Birch, ash, sycamore, and alder were all very severely and about equally damaged but seldom so completely shorn of crown and branches as poplar. Beech were also severely damaged, but seldom seriously except in the case of very old trees. Oak was damaged in a similar manner to beech but usually to a somewhat less extent. Elm received much less damage than might have been expected. This was probably accounted for by the narrow angle and stiff habit of branching and to the fine twigs holding relatively little ice. Conifers in this category generally suffered little damage compared with hardwoods.

2. *Middle-aged Plantations at Normal Forest Spacings.*

Reports received under this heading have been rather conflicting and it is obvious that, even at similar elevations, there has been a considerable variation in the amount of damage done from place to place. With the exception of plantations at high elevations, say over 700 feet above sea-level, it may be safely said that, apart from a few isolated cases, the only species which suffered irreparable damage were poplar, birch, and ash. At elevations of over 700 feet, birch, ash, and sycamore showed the most severe damage in the few places where they were met with in plantations. Douglas fir, European and Japanese larch were often very severely broken, especially in shelter belts running over the 1,000 foot contour. Some such belts were reduced to a shattered wreck with not an unbroken tree left standing. Norway spruce, Sitka spruce, and Scots pine were also severely broken but rather less than the larches. Below

700 feet, many pole stage plantations were badly broken along the windward edge, but on going through the wood it was found that the general damage only amounted to scattered broken tops.

3. *Young Plantations.*

On the whole, it was seldom that severe lasting damage was done to closely spaced hardwood plantations. It was when young trees occurred at very wide spacing, such as the young ash and oak at Savernake, that severe damage took place. Alder and birch, however, showed very heavy damage at high elevations, even when closely spaced.

The most spectacular and, from the economic point of view, the most serious damage caused by the glazed frost was that affecting young plantations of conifers in the thicket to small pole stage. Japanese larch and Douglas fir were the most severely damaged species with European larch a close second. Scots pine and Corsican pine were seldom so broken as Douglas fir or larches at similar elevations, but they were very severely damaged at high elevations in some forests. Sitka spruce suffered occasional severe damage, but more usually sporadic, and so, insufficient to spoil the final crop. Norway spruce received rather less damage than Sitka, probably due to the shorter foliage.

Of the various other species noted, *Abies nobilis* and *Abies grandis* were particularly free from damage; *Cupressus macrocarpa* were rather badly broken when from 10 to 20 feet high; *Thuja plicata* in the pole stage were badly damaged at high elevations (26), but at low elevations were little affected by the ice; *Cupressus Lawsoniana* and *Tsuga* appear to have received relatively little damage. *Alnus incana* at Buriton, Hants, were observed to be much more heavily damaged than *Alnus oregona* in adjoining plots.

TYPES OF DAMAGE (WITH NOTES ON RELATIVE FACTORS).

The five main types of damage caused by the weight of ice are essentially related to locality factors, species, and size and condition of crop.

1. *Trees completely smashed.*

This category refers to stems broken off well below the crown in the case of conifers and some hardwoods, while in other hardwoods the main stem was left standing but was completely shorn of branches. This type of damage was mainly restricted to one of the following three classes:

- (i) Older plantations and shelter belts at elevations over 1,000 feet.
- (ii) Isolated or widely spaced old hardwoods.
- (iii) Poplars.

A block of 33-year-old Douglas fir at Lake Vyrnwy was an exception to these three classes, the elevation here being only 900 feet.

2. *Trees laid flat.*

In this category stems were usually bent right over just above the ground with occasional cases of uprooting and breaking off. Larches and, to a less

extent, Douglas fir seemed to be particularly liable to this type of damage when between 15 and 35 feet high. Data regarding this type are rather confusing, but it appears that this form of damage:

- (i) Very seldom occurred extensively below the 800-foot contour, and, given trees of similar height, increased with the elevation provided slope remained the same.
- (ii) Was most severe on that aspect facing the wind—usually east, but varied somewhat in mountainous country.
- (iii) Was most severe on steep or fairly steep slopes.
- (iv) Occurred only with more flexible species such as larch. Scots pine under similar conditions broke off about half-way up.

Note: An indirect type of forest damage might be mentioned here; namely, the very extensive damage caused to walls and fences by whole trees or heavy limbs falling upon them.

3. *Stem broken half-way down or below, but some live branches remain on tree.*

This was really similar to type 1 but applies to young trees 10 to 25 feet high instead of to the more mature trees. It occurred on pines and spruces in similar situations and conditions to those which produced type 2 damage with larch. With Douglas fir this form of damage is usually intermixed with type 2.

At Savernake, young oak and ash at wide spacings often suffered in this way.

4. *Tops broken but at least part of the live crown remaining.*

This is the commonest type of damage and is divided into two main classes:

(i) Affecting conifers of all sizes from 6 feet upward and varying greatly in intensity. In very young stands it will probably not do much permanent damage; in rather older stands serious crooks will result, but it is hoped that most of these can be removed in thinnings; in old woods the breakage is not of great importance, as it is above timber height.

(ii) Affecting isolated or widely spaced hardwoods and those edges of standing woods which faced the wind. This is the form of damage that is so obvious in the hedgerows and parklands all about the country. It is the dominant type of damage at Savernake. It occurs mainly, and sometimes solely, on the windward side of the tree and varies in intensity from what amounts to a thinning out of the crown on one side to the complete shattering of one half of the crown with heavy thinning of the other.

5. *Trees leaning or bent over but not actually broken, or at an angle of less than 45° to the vertical.*

This last type of damage has affected all classes of trees, the extent of the damage mainly depending on the size of the crop. In young plantations some trees may recover on their own, but staking or wiring will often be necessary. In older stands little can be done except to remove as many as possible of the worst examples in thinnings. There were many cases where the tree itself remained upright but the top section was bent over. In the case of only slight

bends recovery may be complete after a year or two, but where the angle was greater and resin exudation occurred at the bend, it seems probable that a permanent kink will result.

NOTES ON FACTORS AFFECTING ALL CLASSES OF DAMAGE.

(a) *Aspect.* Aspect proved to be of very great importance, and all classes of damage were very much more severe on those slopes, edges of woods, or sides of isolated trees which faced the wind.

Over the majority of the country affected the wind direction was between east and south-east, but over some areas it was north-east. In mountainous country, such as Wales, there was considerable local variation in wind direction owing to deflexion caused by mountain flanks and curving valleys, and in such districts there are examples of severe damage on almost all aspects.

(b) *Elevation.* In practically all cases the degree of damage was directly proportional to the elevation, provided other factors, such as steepness of slope, species, size and condition of crop, &c., were similar. It should be observed, however, that several forests reported that the greatest damage was not at the highest elevation. It was found that this was either because the crops at the higher altitudes were much smaller than those below, or because the slope was steep at the lower elevations and flatter at the top. A further exception occurred where a stronger wind than usual prevented the maximum ice deposit from forming on the leaders and highest branches.

(c) *Slope.* Steepness of slope was of great importance, especially in type 2 damage (trees laid flat).

Three main factors accounted for the fact that the degree of damage usually increased with the slope:

- (i) The inevitable one-sided crown development of trees planted on a steep slope led to the burden of ice being almost wholly on the lower side of each tree.
- (ii) Added to this was the fact that a large percentage of the trees already had a slight inclination down the slope.
- (iii) Rooting is often defective on steep slopes, and even with the ground frozen a few trees went over, carrying many others with them.

(d) *Wind Force.* Except for the case mentioned under heading (b) 'elevation', damage varied directly with wind strength. When the thaw started and released the individual crowns of the trees which had been welded together by the ice coating, it only required a slight wind to bend tall trees sufficiently out of the perpendicular to cause either the snapping off of the top or the bending over of the whole tree.

(e) *State of Ground.* The fact that in most places the ground was frozen solid and held the roots in an iron grip undoubtedly saved many hundreds of acres from complete disaster.

(f) *Height of Crop.* Height growth affected not only the amount of damage but also to a great extent the type of damage. Trees below 8 feet high were seldom very severely damaged. The greatest amount of damage occurred to

crops between 15 and 35 feet high, and almost all cases of areas laid flat came into this category. The reason would appear to be that at this stage the trees are making their maximum height growth, and the diameter growth is not adequate to withstand any extraordinary weight upon the crown. Older woods, 35 to 70 feet high, often suffered broken tops but were only badly shattered at high elevations.

(g) *Density and Condition of Crop.* Although, generally, isolated or widely spaced trees were the most severely damaged, it is significant that all those stands which were laid flat were either densely stocked or had been thinned only just before the glazed frost occurred.

A major factor on all sites was uneven height growth, and, in both young and middle-aged plantations, dominant trees with large crowns overtopping their neighbours always showed the most severe damage. This was particularly noticeable in young stands of Sitka spruce and Douglas fir. In older plantations uniform crops of co-dominant trees suffered less than crops of uneven height growth.

It is evident that adjoining crowns of equal height gave each other mutual support. In the older woods the more open the crop generally the greater the damage, but middle-aged plantations which had been badly under-thinned form a notable exception in that they suffered heavily.

(h) *Elasticity of Wood.* Elasticity proved to be more of a drawback than a benefit; such species as larch and ash suffered severely because they easily started to bend out of the vertical, and, once started, the weight of ice was such that they went right over past the point of possible recovery.

NOTES ON THE DAMAGE IN VARIOUS FORESTS.

The following notes cover some of the most severely damaged areas. Wherever possible, figures are given to show the elevation at which the damage occurred, and in some cases approximate areas are given as well.

Lake Vyrnwy Forest (Montgomery).

This forest, which lies between 900 and 1,500 feet above sea-level, was very severely affected; several hundred acres were seriously damaged, a large proportion of these plantations having to be clear-felled.

Middle-aged Douglas fir planted 1906-8 near the edge of the lake on a slope having a north-north-eastern aspect were ruined, over 50 per cent. of the stems being snapped off about half-way down, or slightly lower, and practically all the remainder having broken leaders and crowns. Many of these trees were 5-9 inches diameter at the point of fracture. Younger Douglas fir planted in 1925 were also completely ruined on some eastern aspects, the whole crop going down in an inextricable tangle of broken, uprooted, and bent-over trees. Similar damage occurred to Sitka spruce and larch in some compartments, but it was not quite so devastating as in the case of Douglas fir. Corsican pine suffered badly as regards broken leaders, but in many cases only a short length was lost and a considerable proportion of the affected trees may produce new leaders.

Norway spruce, although now and again damaged, were on the whole remarkably free from breakage, in striking contrast to Douglas fir or larch on exactly similar sites. Natural birch scattered on the upper mountain slopes and occasionally in the valleys were severely shattered. In general, Douglas fir was the worst-damaged species, larch and Sitka spruce the next. Norway spruce were seldom badly damaged.

Kerry Forest (Montgomery and Salop).

This was another severely damaged area. Practically the whole forest is over 1,000 feet elevation and many compartments lie between 1,300 and 1,600 feet. Almost all the old (acquired) woods have been ruined and are being felled. Of the young plantations over 25 acres were completely devastated and will have to be replanted. A further 150 acres were very severely damaged and 700 to 800 acres received scattered damage, especially to dominant trees. European larch and Douglas fir were the most damaged species; Sitka spruce, Norway spruce, and Scots pine were often quite severely affected.

Cwmeinion Forest (Cardigan).

Very severe damage occurred to plantations between 800 and 1,400 feet elevation. Japanese larch received particularly bad injury. Norway spruce and Sitka spruce were fairly heavily damaged.

Tarenig Forest (Cardigan and Montgomery).

The elevation here is between 1,000 and 1,500 feet. Japanese larch planted in 1929 were severely damaged, and in the older (acquired) European larch plantation every tree had its top broken.

Ceiriog Forest Garden (Denbigh).

This has an elevation of 1,000 to 1,250 feet. The aspect varies from north to south-east but is mainly north-east. Devastating damage occurred to the majority of the plots of the original planting (now about 30 years old). Japanese larch, European larch, and Douglas fir were the most severely affected species; Scots pine and Corsican pine were very badly injured; sycamore and oak also received bad damage; Sitka spruce were also severely affected, but Norway spruce rather less so. *Abies nobilis*, *Abies grandis*, and *Picea omorika* were all very free from damage, particularly *Abies nobilis* (26). Reports indicate that in this immediate district there was relatively little damage below the 900-foot contour.

Mortimer Forest (Hereford, Radnor and Salop).

There was some extremely severe damage in this forest, particularly to Japanese larch, European larch, Douglas fir, and Scots pine. Bad damage occurred at from 500 to 800 feet elevation, but all the worst areas were between 900 and 1,200 feet. In all, approximately 64 acres have been ruined, 129 acres

severely damaged, and over 200 acres less severely damaged. Mature ash and birch suffered very badly.

Radnor Forest (Radnorshire).

This is another forest which received very heavy damage, mainly between the 1,000- and 1,500-foot contours. About 25 acres have been devastated and 160 acres severely damaged, and a large area less severely affected. In young plantations Japanese larch and Douglas fir were most damaged. In old shelter belts, many of which were completely shattered as if by shell-fire, European larch and Scots pine suffered very considerably.

Walcot Forest (Salop).

In this forest some 44 acres have been ruined, 15 acres severely damaged, and 57 acres less severely damaged. Damage occurred at elevations between 800 and 1,300 feet.

Dovey Bryncynfyl Forest (Merioneth and Montgomery).

Severe ice damage occurred above 750 feet elevation. European larch and Douglas fir were mainly affected.

Dovey Corris Forest (Merioneth and Montgomery).

Mature oak were badly smashed and broken. Japanese larch planted 1928-9 were damaged.

Dovey Valley Forest (Merioneth and Montgomery).

Severe damage occurred above the 750-foot contour, particularly to Japanese larch and Douglas fir and to the older European larch acquired plantation.

Dyfnant Forest (Montgomery).

At elevations over 800 feet mature oak were badly smashed and natural birch and rowan badly broken. Japanese larch and Douglas fir, planted 1931-2, were damaged.

Hafod Fawr Forest (Merioneth).

Severe damage occurred to old plantations and to Japanese larch sample plots at 1,100 to 1,480 feet above sea-level. Japanese larch was the species most affected in this forest.

Clocaenog Forest (Denbigh and Merioneth).

The old mixed plantation (pine, spruce, sycamore, &c.) at Is-Gaer-Wen, elevation 1,500 feet, sustained serious injury; otherwise there was relatively little damage. Japanese larch, Scots pine, and *Pinus contorta* received broken leaders to the extent of 2-10 per cent. Sitka spruce and Norway spruce often had their leaders bent but seldom broken. Over most of the high ground of this area the crop was not tall enough to have suffered the worst types of damage.

Beddgelert, Gwydyr, Wyre, Haugh, Cannock, Myherin, Mathrafel, and Brynmawr Forests.

All these forests, although lying within the area affected, were reported to have received relatively little damage. In some cases this is certainly due to the fact that at the higher elevations the tree crops are small.

Quantocks Forest (Somerset).

Fairly severe damage took place in large areas of 15- to 16-year-old conifers, mainly by the snapping off of tops. Old hedges and isolated mature trees were heavily damaged.

Savernake Forest and District (Wiltshire).

Damage occurred at elevations from 450 to 650 feet in the forest and from 400 to 800 feet in the district. The damage, although serious, was not nearly so severe as in many of the high elevation areas in Wales. Injury was due mainly to two factors: (i) wide spacing, and (ii) age of crop. A large area of Savernake Forest is covered by very widely spaced old oak, beech, and ash with some birch, and these trees suffered severely, the majority losing several large limbs and many being reduced to shattered wrecks.

Another class that suffered was the widely spaced young saplings of oak, ash, and beech varying from 12 to 25 feet high. These were frequently snapped off at from 6 to 12 feet above ground-level, sometimes leaving scarcely any live branches or twigs and often splitting the stem for a length of several feet.

In this district conifers received very little serious damage. Of the hardwoods, poplar, birch, ash, beech, and oak all suffered severely. Elm and sycamore were much less damaged.

Buriton Forest and Petersfield District (Hampshire).

Little severe damage occurred below 400 feet elevation except to poplar. Between 400 and 700 feet severe damage was inflicted on old hardwoods, especially birch, beech, and ash. Only relatively slight damage was received by young plantations at Buriton Forest except for numerous broken tops in alder, birch, and European larch in the experiments on Holt Down (600 feet); these trees were from 12 to 25 feet high.

Forest of Dean Division (Gloucestershire, and Monmouth).

Taken as a whole, there was little serious damage in this division. The ice deposit appears to have been a good deal less than in many districts. Below the 450-foot contour there was seldom any bad injury except to very old hardwoods. A few cases of severe breakage were reported at elevations between 600 and 900 feet from Trelleck Common, Chepstow Park, the Beacons, Stapledge, and Abbotswood. The species mainly affected were:

Hardwoods: birch, beech, and old oak, principally at over 600 feet elevation.

Conifers: Japanese larch and European larch the most seriously affected;

Sitka spruce occasionally; Scots pine and Corsican pine mainly only where

previously weakened by Pine-shoot moth; Douglas fir only where the crop was abnormally dense; Thuya and Norway spruce stood up very well.

New Forest Division (Hants., Wilts. and Dorset).

No severe damage was reported except at Gardner Forest, where 3 acres of 20-year-old birch suffered severely.

GENERAL SUMMARY.

Extent of damage (Forestry Commission Areas only).

Acreage figures have not been received for all forests in the affected areas, and the following estimates can be taken as probably erring on the under side.

	<i>Acres</i>
Damage so severe that complete clearing and replanting will be necessary. (It should be noted that this figure does not include the numerous old shelter belts that were completely shattered. Neither does it include a good many small areas of acquired woodland that were irreparably damaged.)	Over 500
Damage severe, but does not justify complete clearing.	Over 1500
Damage less severe and mainly consisting of numerous broken and badly bent leaders in young plantations, but sufficiently good trees remain for a fair crop.	Over 5000

Degree of injury to Various Species.

Hardwoods: Poplar—probably the most severely damaged.

Birch, ash, sycamore, and alder—very severely damaged.

Beech—severe damage.

Oak—usually rather less than beech.

Elm—much less damage.

In all cases the damage to hardwoods was most severe where the trees were old and very widely spaced or isolated.

Conifers: Japanese larch and Douglas fir—these two species were the most severely damaged.

European larch—often severe injury but seldom as bad as Japanese larch or Douglas fir.

Sitka spruce—often severe damage but less than larch or Douglas fir.

Scots pine and Corsican pine—sometimes very severe damage at elevations over 1,000 feet., and at lower elevations if previously weakened by Pine shoot moth.

Norway spruce—not often severely damaged except in exposed shelter belts at high elevations.

Thuya—in general, not much damaged, but where it occurred at high elevations was considerably affected.

Abies species, Lawson's cypress and Tsuga—very seldom damaged seriously; *A. nobilis* particularly free.

Main Factors affecting Damage.

(i) *Thickness of Ice Coating.* Seldom much severe damage, except to very old hardwoods, when ice coating was less than 1 inch thick. The most severely damaged areas had ice from 2 to 4 inches thick, but some severe damage was caused by ice 1 to 2 inches thick. It is important to distinguish between solid ice and rime, the latter being a much lighter coating than solid ice.

(ii) *Elevation.* The really devastating damage practically always occurred above the 1,000-foot contour. Seldom was there any bad breakage below 400 feet, but many cases of severe damage occurred between 500 and 1,000 feet.

(iii) *Aspect.* The wind was mainly easterly and the worst damage usually occurred on eastern aspects.

(iv) *Slope.* The steeper the slope the worse the damage, other factors being equal.

(v) *Wind Force.* The stronger the wind the greater the damage, except for a few cases where a particularly strong wind prevented the maximum ice deposit from forming on the leaders and upper branches.

(vi) *State of Ground.* The frozen ground, by gripping the roots, undoubtedly saved many hundreds of acres from complete disaster.

(vii) *Height of Crop.* Trees below 8 feet high were seldom seriously damaged. The greatest damage occurred to young crops between 15 and 35 feet high and to older woods and shelter belts 35 to 70 feet high.

(viii) *Density and Condition of Crop.* Damage was worst to:

- (a) Isolated or widely spaced old hardwoods.
- (b) Densely stocked young plantations or such plantations which had just been heavily thinned.
- (c) Plantations of very uneven height growth. In such areas it was always the tallest trees that suffered the worst injury.
- (d) Young saplings at very wide spacing such as are met with at Savernake Forest and in many parklands.
- (e) Middle-aged plantations which had been inadequately thinned.

PREVIOUS RECORDS AND GENERAL OBSERVATIONS.

Fortunately for British forestry, a glazed frost of the intensity experienced in January 1940 is an extremely rare phenomenon. There are, however, several on record, including the following:

1868. Dartmoor—referred to as 'Ammil' (7).

1889, 7 January. Norfolk—referred to as 'Rime' (23).

1903, 17 January. London, Haslemere, Barnet, Cirencester, and Southport—referred to as 'Silver thaw'. Reported to have caused many street accidents (22).

1907, December. Sheepstor, Dartmoor—referred to as 'Ammil' (7).

1912, 17-18 January. Wrotham and Sutton Valance, Kent—very local, referred to as 'Frozen rain' (5) and as 'Glazed frost' (4).

1912, 3 February. Hereford—referred to as 'Silver thaw' (11).

1912, 3 December. Edinburgh—called 'Silver thaw' (29).

1914, 21-22 December. Duns, West-Witton, Yorks. (3).

1927, 21 December. London—reported as the 'worst glazed frost since 1903'
—and many other parts of England (7, 10).

1927, 29 December. Dartmoor—referred to as 'Ammil' (7).

1934, 24 February. Rickmansworth (17).

1936, 11 February. Fareham and Isle of Wight (28).

Glazed frosts appear to occur more frequently and with greater severity on the Continent. There are many records of extensive damage being caused to forests in Germany and France. Mr. W. R. Fisher (13) states that a most destructive ice-break occurred in November 1858 in the Spessart, Odenwald, part of the Bavarian Palatinate and Rhenish Prussia, in which the ice crust was eighteen to twenty times the thickness of the wood on which it rested. The amount of damage caused appears to have been enormous. He also refers to extensive breakage of woods by ice in January 1879 in France and central Germany. In this glazed frost it is recorded that in carefully thinned Scots pine woods the number of stems broken was as high as 70 per cent., and in certain broad-leaved forests 50 per cent. of the trees were shattered. The Forest of Fontainebleau appears to have been severely affected; here, thin twigs and telegraph wires carried ice up to 8 inches in diameter. Mr. C. J. P. Cave also discusses this particular glazed frost (9). There is no doubt that the phenomenon on this occasion was of a similar nature to the 1940 glazed frost. Observers have recorded that rain froze immediately on contact with solids, even warm objects; however, when heavier rain was falling there was a certain amount of water running over the object before turning into ice, and there was some icicle formation. This glazed frost was undoubtedly extremely severe and there are several accounts of its occurrence and the resulting damage (27).

The phenomenon is by no means unknown in North America (1, 18, 19). Dr. Boyce states that injuries caused by the severe ice storm of November 1921 in New England were still in evidence 10 years later (6). In March 1940 a glazed frost appears to have occurred in the New York metropolitan area. It is reported that the weight of ice broke off the tops and limbs of thousands of trees which ranged from saplings to large oaks. Telephone communications were broken down and fire-alarm systems and electric power stations were put out of action (14). More recently, in December 1940, a very severe glazed frost occurred in the Texas Panhandle which is a high plateau of 4,000 feet elevation (2). There was no wind, the temperature was hovering around the freezing-point, there was a drizzle, and the drops of moisture froze on trees and telephone wires, causing a considerable amount of damage.

In the British Isles, however, the fact that widespread glazed frosts are so exceptional makes any discussion of prophylactic measures almost superfluous. None the less, it is worth noting that in some of the cases of severe damage recorded in the present paper, the plantations would probably have suffered much less severely if the silvicultural treatment had been more in accordance with accepted principles. At elevations over 1,000 feet the damage was clearly

of the nature of an 'Act of God' which no silvicultural methods could avert. It is fortunate that the risk of another glazed frost of similar intensity is sufficiently remote to justify the forester leaving this particular hazard out of his calculations.

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Photo by Dennis Moss

Hedgerow with ice coating. Ash in foreground bent to ground by weight of ice.



Photo by Dennis Moss

Young Abies showing ice coating on foliage.



Photo by W. A. Cadman

Top of 6-year old Japanese larch bent over by weight of ice. Brynmawr Forest, Cardiganshire. (See also Plate XIV).



Photo by W. A. Cadman

Wires, heather, and grasses encased in ice at 800 ft. Brynmawr Forest.

PLATE IX



Photo by Dennis Moss

Young Lawson's cypress, ice coated and bent over.



Photo by Dennis Moss

Young Lawson's cypress, almost returned to upright position after thaw.



Photo by Dennis Moss

Young Cedar, ice coated and bent over



Photo by Dennis Moss

Young Cedar, almost returned to upright position after thaw.



Photo by W. A. Cadman

Japanese larch, 6 years old, weighed down by ice. Elevation 800 ft. Brynmawr Forest.



Photo by Dennis Moss

Typical one-sided damage to Elm.



Photo by R. C. B. Gardner

Widely spaced Oak saplings decapitated by the weight of ice. Savernake Forest, Wilts.



Photo by R. C. B. Gardner

Remarkable damage to old Beech in Savernake Forest.



Photo by R. C. B. Gardner

Sycamore split asunder in Savernake Forest.



Photo by M. Nimmo

Typical damage to 13-year old Douglas fir in Radnor Forest, Radnorshire.



Photo by R. C. B. Gardner

Devastating damage to European larch near Clun, Shropshire. Elevation over 500 ft.



Photo by M. Nimmo

Damage to European larch shelter belt at 1,400 ft. Trees broken by the weight of ice, Radnor Forest.

THE UTILIZATION OF SOFTWOOD TIMBER DAMAGED IN THE GLAZED FROST, 1940

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THE GLAZED FROST OF JANUARY, 1940.

THE opportunity has recently been taken to investigate the damage done to standing timber in an area severely affected by the glazed frost or ice-storm of 27-29 January 1940. The meteorological conditions responsible for the phenomenon have been discussed elsewhere (2, 6, 7), but they are sufficiently remarkable to be recounted briefly before describing the effects on trees and timber. It seems that the rain which began to fall on the evening of 27 January must have passed through a layer of cold air and been cooled to below 32° F. without freezing, with the result that the rain-drops turned into ice immediately they landed on anything solid. All exposed surfaces became covered with ice which grew thicker as the precipitation went on more or less continuously until the 29th. Telephone wires and blades of grass were in very many instances encased in cylinders of ice over an inch in diameter, and twigs and branches of trees were similarly coated. As a general rule it was on the higher ground that the heaviest deposit of ice was formed. Here the coating on twigs and branches was anything up to about an inch in diameter below 500 feet, and up to 3 or 4 inches at higher altitudes.

The area affected appears to have extended west to east from near the Welsh coast and south Devon to Cambridgeshire and east Sussex, and north to south from Cheshire to the coast of the Channel. Salisbury Plain, the Mendips, the Cotswolds, Marlborough Downs, and the mountains of central and north Wales were all districts of very heavy ice deposit.

NATURE AND EXTENT OF DAMAGE TO STANDING TIMBER.

The damage sustained by plantations and individual trees has been described in published reports (4, 6, 7, 12, 13) and in the records of the Forestry Commission. They deal principally with the silvicultural aspects of the matter, namely, the way in which the growth of the trees has been affected and the future treatment of damaged plantations. The present paper is concerned rather with the utilization of damaged timber and the effects of the frost on the quality of timber which is being allowed to grow on. This latter consideration applies to large areas of plantations which to all appearances have not been seriously affected. The investigation has been confined to softwoods mainly in the pit-prop and pole stages, but some of the conclusions are applicable to timber of larger size.

The accumulation of ice on every needle, twig, shoot, and branch resulted

in the trees being bent, bowed down, or broken by the abnormal weight. Reports from different parts of the country show that in young plantations, although the trees were bowed to the ground, they generally recovered almost completely after the thaw. The Forestry Commission's survey has shown that there was rarely any severe visible damage to trees below 8 feet in height. Many older stands, however, suffered permanent damage which varied according to age, species, and exposure. The greatest damage was to trees between 15 and 35 feet high (12).

The commonest type of permanent damage seems to have been the breaking off of tops and leading shoots. Where this is not so severe as to preclude recovery, the effect of the damage may be no more than a kink in the main stem. In more serious cases it will be better to clear-fell than to leave badly maimed trees to grow into misshapen timber. Less common, but extensive enough to be very serious, is the irreparable injury to trees which have had their main stems permanently bent or broken at varying heights above the ground, or have been completely uprooted. Uprooting was general in some stands, notably those of Douglas fir. Fortunately, over a large part of the area the ground was frozen hard so that the roots were held fast in the soil. There is no doubt that this averted enormous losses which would have resulted from defective root systems in soft ground and under great strain.

PREVIOUS RECORDS OF SIMILAR DAMAGE TO TIMBER.

There appears to be no previous record in forestry literature of any tests or systematic investigations on timber damaged in glazed frosts. Reports by continental investigators of similar effects resulting from snow and wind damage, however, show that apparently sound stems are liable to contain failures which may seriously reduce the strength of the timber. Burger (1) reports that apparently unaffected timber from a wind-damaged stand of Silver fir in Switzerland was found to break suddenly under slight strain when used for props; the sawyers also noticed that boards cut from apparently sound logs were easily broken. Investigation showed distinct signs of compression and splits in logs which, judged by external appearances, were perfectly sound. Reports of similar defects attributed to wind damage in Switzerland and Germany have been recorded for various species of softwood (8, 9, 14, 16, 17). They agree that failures generally occur on the compression side of the tree at intervals of 12-32 inches; these tend to occur at whorls where the branches or knots are large and may extend from the cambium inwards nearly to the pith; the lower part of the bole is generally unaffected. In spruce, injury to the stem is sometimes indicated by resin exudation on the outside of the bark. These reports also confirm that the strength of affected timber is liable to be impaired, as evidenced by trees in wind-damaged areas being broken in felling, and sawn timber from such logs giving way suddenly under slight strain. Mechanical tests on specimens cut from damaged spruce showed marked reduction in strength, particularly in bending and tension (16).

The type of failure described and illustrated by these investigators is clearly

a compression failure such as occurs on the inside of a bend. Similar failures are a well known phenomenon in certain species of tropical timbers and have been ascribed to storm damage affecting the trees in early life (11). They are comparatively rare in trees of the temperate zones, presumably on account of their relative immunity from severe storms such as occur in tropical climates.

INVESTIGATION OF DAMAGE TO TIMBER.

In view of the reports just referred to, it was considered advisable to investigate the extent of the damage in apparently sound timber in plantations known to have been affected by the glazed frost of January 1940. The primary object of the investigation was to see how far such timber could safely be utilized for structural purposes, especially pit-props. At the same time, it was proposed to examine the effect of the damage on the various mechanical properties of the wood and also on the subsequent growth of the timber.

Description of Site.

On the advice of the Forestry Commission an area in central Wales, showing various types of damage to several different species, was selected for the investigation. This area had been inspected by an officer of the Forestry Commission since the catastrophe, and his report greatly facilitated the selection of representative material for test. The plantations in question cover an area of some 5–6,000 acres, mostly established within the last 30 years. There are some older trees which are now yielding saw logs, but the great bulk of the damaged timber is destined for conversion into pit-props, poles, and small material for estate work.

Description of Material.

It was decided to select representative material of Japanese larch and Douglas fir, being two of the species which had suffered most severely, for examination and test. Twelve trees of Japanese larch were selected from a plantation with an average d.b.h. of about 5 inches, established in 1920. This was situated at an altitude of about 1,050 feet, on a steep hill-side with a north-west aspect. In the area sampled about 50 per cent. of the trees were severely damaged, the stems being bowed through as much as 90° or broken off at 8–15 feet above the ground. The usual type of break was a short fibrous fracture extending only a few inches along the grain. Sample trees showing both types of damage were taken together with stems which had been bowed over by the weight of ice and had subsequently recovered. Portions of four Douglas firs were selected from a devastated plantation situated at an altitude of about 1,000 feet with a north-north-east aspect. This plantation was established in 1906–8 and was in process of being cleared. The average d.b.h. varied from 5 to 10 inches. In the area sampled well over 50 per cent. of the trees were uprooted or snapped off at varying heights above the ground, practically all the remainder having broken leaders and crowns. In contrast to the larch, the broken Douglas firs showed long shear failures often with

splits running considerable distances up and down the stem, the timber from such badly shattered butts being useless for anything but fencing stakes and the like. In addition to the material taken from the standing trees, 32 pit-props of Douglas fir, in diameters ranging from 3 to 7 inches, were taken at random from consignments cut on the same area for delivery to the collieries.

Examination at the Laboratory.

On arrival at the Laboratory the specimens were carefully barked and the wood examined for signs of mechanical injury.¹ (Trees which had put on a year's growth since the time of the frost had the outermost ring of wood removed also.) The exposed wood surface showed closely spaced criss-cross markings characteristic of incipient compression failure, sometimes quite conspicuous, but more often fine and indistinct and likely to pass unnoticed by a casual observer. Nearly all the specimens cut from broken or severely bent stems showed these signs of incipient failure in varying degrees of intensity, as also did some of the specimens cut from the erect, apparently undamaged trees and some of the Douglas fir pit-props prepared for consignment to the collieries. These markings, when present, were observed to occur more or less continuously up and down the compression side of the stem, in some cases from within a foot or so of the ground to a height of 20 feet; in others they were confined to a comparatively short length of the stem in the region of the greatest stress. The more pronounced compression failures, as described above in wind-damaged trees, were only occasionally present and were usually associated with knots (see Fig. 3).

The distribution and intensity of the failures were recorded and the greater part of the material was then cross-cut to lengths approximately equal to twelve times the minimum diameter, this being the slenderness ratio usually required with pit-props. The remainder was reserved for the preparation of small clear test specimens. The props were then tested in compression according to the procedure previously followed at the Laboratory.

Mechanical Tests on Pit-props.

The results of the tests on the pit-props are shown in Table I. For comparison, the results of previous tests on normal, undamaged props of the same species carried out at the Laboratory in 1930 (3) are included.

It was apparent from the tests that the influence of the incipient compression failures on the strength of the props was in general slight compared with that of knots and natural bends in the props. There was some indication, in the case of the Japanese larch, that the fibre strength at the limit of proportionality was affected by the failures, but with the relatively small number of props tested it was not possible to show a positive correlation supported by statistical analysis. The conclusion drawn from the test figures is that the strengths developed in the props were within the range that might have been expected of undamaged props.

¹ 'Mechanical injury' in this paper refers to stressing beyond the limit of proportionality.

These results were somewhat surprising in view of reports by previous investigators of severe compression failures and considerable reduction in strength in trees damaged by wind storms. The deformation of many of the trees

TABLE I. *Results of mechanical tests on pit-props in the green condition (mean values)*

<i>Species</i>	<i>Origin</i>	<i>No. of props tested</i>	<i>Fibre stress at maximum load (lb. per sq. in.)</i>	<i>Fibre stress at limit of proportionality (lb. per sq. in.)</i>
Japanese larch	Damaged plantation (1941)	13	2,574	1,485
„ „	Undamaged plantation (1930)	14	2,510	1,730
„ „	Undamaged plantation (1930)	19	2,430	1,740
Douglas fir	Damaged plantation (1941)	7	3,180	2,169
„ „	Damaged plantation (1941)	13	2,835	1,856
„ „	Undamaged plantation (1930)	12	2,190	1,440
„ „	Undamaged plantation (1930)	16	2,150	1,560

affected by the glazed frost must have been as great or greater than in the case of trees badly damaged by wind action. The probable explanation of the less severe damage in the former is that there was no swaying of the trees such as would normally occur in a wind storm, so aggravating the effect of the initial failures by alternating tensile and compressive stresses tending to produce a complete separation of the fibres extending from the cambium inwards towards the pith.

Mechanical Tests on Small Clear Specimens.

To investigate the effect of the incipient compression failures on clear timber free from knots and irregularities of the grain, small test specimens, $\frac{5}{8}$ inch square in cross section, were prepared from selected portions of some of the damaged trees. Billets of convenient length were cut from between the knot whorls and cleft so as to give straight-grained blanks for the preparation of the test specimens. Those from the compression side of the tree, with more or less pronounced compression failures, were tested in comparison with sound specimens from the opposite, or tension, side.

The results of these tests are summarized in Table II, where, in addition, results of standard laboratory tests on small clear specimens of undamaged wood of the same species are included for comparison. The mean values for both species show that in ultimate bending strength, as expressed by the equivalent fibre stress at maximum load, there is no significant difference

between the two sides of the tree. The stiffness appears to be impaired considerably, the reduction in the modulus of elasticity of the wood from the compression side being very marked. There is no significant decrease in maximum compressive strength, while toughness shows a slight reduction. Toughness is a strength property with considerable variation and in consequence reductions of the order exhibited by the wood from the compression side are not significant. Statistical analysis shows that the only strength property to be affected to a significant extent is that of modulus of elasticity.

It is pointed out that the above comparison between the two sides of the tree is based on the assumption that the wood on the tension side was not appreciably affected and the 't' values may be taken as being those of normal wood. In this respect the values for undamaged wood from other consignments of larch and Douglas fir included in the table of results, although not strictly comparable, as they refer to standard sizes of specimen, indicate, when allowance is made for specific gravity differences, fairly close agreement with those for the 't' side of the tree.

These results are in general agreement with those of Trendelenburg (16) who found that incipient compression failures in wind-damaged trees had little effect on compressive strength but in bending caused a very considerable reduction in the modulus of elasticity.

Conclusions drawn from Mechanical Tests.

The fact that the specimens selected for test in the form of pit-props showed no serious weakening should not be taken to mean that all affected timber is normal so far as its strength is concerned. In round timber of the dimensions tested, any possible reduction in strength due to incipient compression failures may be masked by the weakening effect of knots and natural bends in the stems.

The results of the tests on small clear specimens, however, indicate that the deformation of the standing trees has appreciably reduced the modulus of elasticity of the wood on the compression side. The ultimate bending strength, the compressive strength, and the impact bending strength (toughness) are not affected to any significant extent. It is emphasized that the material available for these tests was limited in quantity and in view of this and of the reduction in modulus of elasticity it must be concluded that caution is advisable in utilizing timber from stands in severely affected areas.

It is recommended that pit-props should not be cut from badly bowed trees. Props from damaged trees should be barked before inspection and no prop should be accepted if the induced failures are as conspicuous as those shown in Figure 1. Failures appearing as faint etchings, as shown in Figure 2, may safely be ignored. (In the case of props cut from still living trees which have continued to put on wood since the time of the frost, it will not, of course, be practicable to expose the surface of the damaged wood. In any case, the strengthening effect of the rings laid down since the frost will tend to counteract any reduction in strength due to earlier compression failures.) It is further

TABLE II. Results of mechanical tests on small clear specimens in the green condition (mean values)

Species	Specific gravity*	Static bending.			Impact bending.		Compression parallel to the grain.	
		No. of tests	Equivalent fibre stress at maximum (lb. per sq. in.)	Modulus of elasticity (1,000 lb. per sq. in.)	No. of tests	Toughness (in.-lb.)	No. of tests	Maximum compressive strength (lb. per sq. in.)
Japanese larch Tension side 't' Compression side 'c' Percentage increase (+) or decrease (—) of 't'	0.48	7	6,980	899	5	321.3	24	2,990
	0.47	6	7,100	461	8	291.2	24	3,050
	..	..	+1.7%	—48.8%	..	—9.35%	..	+2.0%
Japanese larch Undamaged wood †	0.40	..	6,300	950	..	..	..	2,850
Douglas fir Tension side 't' Compression side 'c' Percentage increase (+) or decrease (—) of 'c'	0.43	18	7,250	1,177	16	127.6	24	3,280
	0.42	12	7,190	771	14	111.2	24	3,370
	..	..	—0.8%	—34.5%	..	—12.9%	..	+2.7%
Douglas fir Undamaged wood †	0.41	..	7,170	1,320	..	..	..	3,340

* Based on weight when oven-dry and volume as tested.

† Tests on 1 in. × 1 in. sub-standard test specimens.

‡ Tests on 2 in. × 2 in. standard test specimens.

recommended that sawn timber showing conspicuous compression failures should not be used for structural purposes where the strength of the timber is of importance.

Deferred Effects of Damage to Standing Timber.

Apart from the mechanical injury to the woody tissues and the resultant weakening of the timber, the deformation of trees affected by the glazed frost may have other adverse effects on the subsequent growth and quality of the timber. The first of these is the development of compression wood, an abnormal type of tissue with characteristic structure and properties commonly formed on the lower, or compression, side of leaning stems of coniferous trees. The presence of well developed compression wood is generally shown on the cross-section of a log by the eccentric growth of the annual rings and the unusually wide, crescent-shaped zones of dense summer wood on one side of the section. Compression wood has an exceptionally high longitudinal shrinkage which is liable to cause serious defects in converted timber and, to some extent, in poles also. Differences in shrinkage between adjacent layers of normal wood and compression wood result in distortion, checking, and splitting. Figure 4 illustrates the cross-section of one of the Japanese larch poles selected for test. This tree suffered a slight permanent bend as a result of the glazed frost, but was otherwise undamaged. The illustration shows the zone of compression wood on one side of the tree formed in the growing season following the frost. Similar compression wood formation was observed in all the bent stems brought in for test, as also in some which did not appear to have been seriously deflected.

It has been shown (10) that an inclination of a few degrees from the vertical is sufficient to stimulate the formation of compression wood, which tends to be more pronounced in vigorous trees. Thus it is probable that a large proportion of the trees permanently deflected as a result of the glazed frost have begun to form compression wood, and that this will continue to be formed for a number of years, depending on the severity of the deflection, until the deviation from the vertical has been corrected.

Another and more unusual result of the particular type of strain in question is the development of callus swellings on the stem at points where the tissues have been ruptured. These have been recorded on storm-damaged spruce and Silver fir in Switzerland and Germany (1, 8, 9, 14, 16). The swellings are due to abnormal local activity of the cambium and presumably have the effect of reinforcing the stem at the points where its strength has been reduced by the injury to the fibres. They become apparent four or five years after the date of injury, or possibly sooner, and must appreciably reduce the value of the timber if they are allowed to develop, as may be judged from the illustrations in the references numbered 14, 15, and 16. These show bulbous swellings at intervals of 12-20 inches throughout the length of the stem. It is not possible to say whether this type of defect is likely to develop in trees affected by the glazed frost, but it will be advisable for foresters to keep a

look-out for them. The appearance of such swellings will indicate the presence of concealed compression failures in the timber and will also be a warning that the form of stems, and hence the quality of the timber, will probably deteriorate as growth proceeds.

SUMMARY.

1. The mechanical damage to standing softwood timber caused by the glazed frost of January 1940 is described.

2. The effect of this damage on the strength of selected material of Japanese larch and Douglas fir has been investigated, with the primary object of ascertaining how far such timber can safely be utilized for structural purposes.

3. Compression failures induced by the weight of ice have little effect on the strength of the timber in the form of pit-props. Tests on small clear specimens, however, show a reduction in the modulus of elasticity of the wood from the compression side of the tree. Some caution is therefore advised in utilizing timber from affected areas for structural purposes, and it should not be used in structures required to carry a long-time load.

4. Apart from possible rupture of the fibres, the quality of the timber in trees permanently deflected as a result of the glazed frost is likely to be adversely affected by the development of compression wood. Callus swellings may develop on stems at points where the tissues have been ruptured.

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FIG. 1. Douglas fir pitprop showing compression failures induced by the weight of ice deposited in the glazed frost.



FIG. 2. Douglas fir pitprop showing faint criss-cross etchings, the first signs of compression failure.



FIG. 3. Japanese larch pitprop showing well developed compression failures.



FIG. 4. Cross-section of Japanese larch showing, in the lower part of the section, a crescent-shaped zone of compression wood formed in the growing season following the glazed frost.

THE VARIABILITY IN RESISTANCE TO DECAY OF THE HEARTWOOD OF HOME-GROWN WESTERN RED CEDAR (*THUJA PLICATA* D. DON.) AND ITS RELATION TO POSITION IN THE LOG¹

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INTRODUCTION.

THE heartwood of Western red cedar has a well-established reputation for high resistance to decay, even under conditions very favourable to attack by wood-destroying fungi. This is borne out both from records of wind-thrown trees, which have remained in sound condition after lying in the forest for long periods, and from the performance of the timber in service; it has been amply confirmed by laboratory tests (5, 3). In all these tests the material has been of Canadian or American origin.

In this country plantations of Western red cedar have only been laid down on any scale in recent years, and consequently little mature home-grown timber is as yet available, apart from a few specimen trees grown in parks and private gardens. However, it was thought desirable to ascertain whether the home-grown timber possesses the same high natural resistance to decay as that shown by imported wood, and, in addition, to investigate how far such resistance varies in different parts of a single tree. Such a variation might explain a number of cases in which severe decay has occurred after a short period of service. In some of these there was evidence of incipient decay in the living tree which might have accounted for the trouble, since indications have already been obtained that such timber is more readily attacked by other fungi, and in particular by *Coniophora cerebella*. This less durable material can often be recognized by its dull-brown colour (4).

Sherard & Kurth (6) have shown that the degree of resistance to fungal attack of the wood in *Sequoia sempervirens* varies according to the position of the tree from which it is taken, and that this variation is associated with the concentration of the water-soluble extractives. The following investigation was undertaken in order to ascertain whether this was also true in the case of the timber of *Thuja plicata* grown in this country. Experimental material was obtained from a tree grown in Sutherland.

The tree selected was about 65 years old, 80 feet high, and just over 2 feet in diameter above the buttressed base. The clear bole from which the test samples were obtained was 30 feet long, this being cross-cut into two lengths of 15 feet each to facilitate transport. Rate of growth was uniform, varying from 4.5 to 5.5 rings per inch with an average of 5.

¹ Manuscript received 29 May 1941.

CONVERSION.

The log was converted into planks, and the samples were taken from the central plank, which included the pith. From this central plank a cross-section was taken at every 5 feet up the plank. Thus six sections were obtained approximately 10.25 cm. deep and 6.25 cm. thick (Fig. 1).

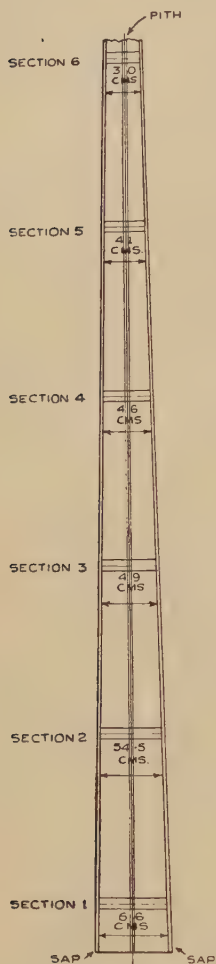


FIG. 1. Diagram illustrating conversion of centre plank into sections.

Centre plank = 30 ft. long $\times$ 2½ in. thick.

After removal of the sapwood the test samples measuring 5 cm. $\times$ 1.25 cm. $\times$ 1.25 cm. were cut from these sections (Fig. 2), the central samples, which included the pith, and any others with knots or other visible defects being rejected. The corresponding samples equidistant from the sapwood on either side of the pith were treated as identical. Thus the samples represented the timber from varying points on the diameter of the tree, excluding the pith, at approximately every 5 feet in height.

SELECTION OF FUNGI.

Trial tests were carried out in order to select suitable species of fungi; this was necessary owing to the difficulty which is often experienced in obtaining appreciable attack on this timber in laboratory tests. As a result of these tests two species were selected, namely, *Polystictus versicolor* (Linn.) Fr., which causes a white rot of many hardwoods and *Poria incrassata* (B. et C.) Burt., representing the brown rot type, a species which causes considerable damage to house timber in America.

Previous experience had shown that consistent attack on Western red cedar cannot be obtained using the standard wood block method of test in which the test fungus is grown on malt agar; therefore, a modified technique was used in which the fungus is cultivated on sawdust, to which an accelerator¹ has been added, as it has been found that many fungi make much more vigorous growth on this than they do on an agar medium (2).

PREPARATION OF FLASKS.

The modified Kolle flasks provided with a reservoir in the neck, as used by this Laboratory in wood preservative tests, were employed. Sawdust of medium particle size of Norway spruce (*Picea abies*) and of beech (*Fagus sylvatica*), to which 5 per cent. of the accelerator had been added, was used as the medium. The total oven-dry weight of sawdust plus accelerator in each flask was 17 g.;

¹ Accelerator: 50 per cent. maize meal, 30 per cent. bone meal, 17 per cent. potato starch, 2 per cent. sucrose, 1 per cent. burnt ash of sapwood of Scots pine, the proportions being by weight.

sufficient water was added to bring the moisture content up to 170 per cent. and a moist pad of absorbent cotton wool was placed in the flask to keep the air around the culture moist. After sterilization equal numbers of flasks were inoculated with each of the two fungi, the flasks containing beech sawdust being inoculated with *Polystictus versicolor*, and those containing Norway

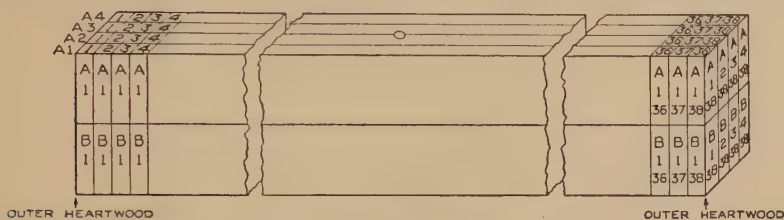


FIG. 2. Diagram illustrating method of conversion of section 1. Size of samples 5 cm. $\times$ 1.25 cm. $\times$ 1.25 cm. Samples marked A were exposed to attack by *Polystictus versicolor*. Samples marked B were exposed to attack by *Poria incrassata*. Sections 2-6 were converted in a similar manner.

spruce sawdust with *Poria incrassata*. The inoculated flasks were kept at a constant temperature of 22° C. in the dark, until the fungus mycelium had permeated the sawdust. The wood samples were sterilized by means of dry heat in an oven at 100° C. for 18 hours, and after having been weighed (oven-dry weight), were placed on glass rests above the fungus mats in the flasks, which were then replaced in the constant temperature room. Whenever necessary the cotton wool pads in the necks of the flasks were re-moistened in order to maintain a humid atmosphere in the flasks.

DURATION OF TEST.

The samples were removed from the flasks after 6 months' exposure to fungus attack and, after careful removal of any adhering fungus mycelium, were oven-dried and then reweighed. By subtracting the figure obtained from the original oven-dry weight of each sample, the actual loss in weight owing to fungus attack was obtained. This loss in dry weight was then calculated as a percentage of the original oven-dry weight. This percentage gives a useful relative measure of the amount of decay.

A summary of the figures is given in Table I. In this table the first column on the left showing percentage losses in weight represents the results based on samples taken from the outermost heartwood adjoining the sapwood. Proceeding from left to right the columns contain results from samples taken from positions progressively nearer the centre of the tree. The figures furthest to the right in each section represent the results from samples taken near the centre of the trunk, but excluding the pith. Owing to the taper of the tree the sections from the upper part of the tree are smaller in diameter, so that fewer groups of samples could be obtained.

In this table loss in weight for individual samples is not given, but the complete figures, including moisture contents for individual samples, are available for reference by anyone specially interested.

TABLE I. *Average percentage loss in weight of samples after 6 months' exposure to test fungi*

No. of section	Height in ft. from base	Average percentage loss from outer heartwood adjoining sap			Average percentage loss from inner heartwood excluding pith			Average percentage loss for all samples in each cross-section
A. <i>Polystictus versicolor</i>								
1	0	..	(a) 1.75 (11)*	(a) 2.24 (13)	4.33 (15)	3.38 (16)	3.31 (55)	
2	5	1.51 (16)	1.46 (16) (1.61) (27)	4.77 (16) (3.51) (29)	5.06 (16) (4.70)	..	3.2 (64)	
3	10	1.15 (15)	2.16 (16)	8.93 (13)	..	..	4.08 (44)	
4	15	1.96 (16)	4.45 (16)	8.78 (13)	..	..	5.06 (45)	
5	20	2.46 (16)	5.88 (14)	7.73 (13)	..	..	5.36 (43)	
Average loss per cent. for all 5 cross-sections		1.77 (63)	3.14 (73) Omitting (a) 3.49 (62)	6.49 (68) Omitting (a) 7.55 (55)	4.7 (31) ..	3.38 (16) ..	4.2 (251) ..	
6	25	4.93 (12)	..	16.84 (8)	..	..	10.89 (20)	
B. <i>Poria incrassata</i>								
1	0	..	(a) 1.23 (13)	(a) 0.55 (13)	0.38 (16)	0.71 (16)	0.72 (58)	
2	5	0.51 (15)	1.62 (16) (1.43) (29)	3.83 (16) (2.19) (29)	8.56 (16) (4.47) (32)	..	3.6 (63)	
3	10	0.38 (16)	1.6 (16)	11.9 (15)	..	..	4.63 (47)	
4	15	0.81 (16)	5.01 (16)	22.06 (16)	..	..	9.29 (48)	
5	20	0.94 (14)	7.72 (16)	21.41 (16)	..	..	10.02 (46)	
Average loss per cent. for all 5 cross-sections		0.66 (61)	3.44 (77) Omitting (a) 3.99 (64)	11.95 (76) Omitting (a) (14.8) (63)	4.47 (32) ..	0.71 (16) ..	5.65 (262) ..	
6	25	0.83 (12)	..	5.13 (11)	..	..	2.99 (23)	

* Numbers in brackets indicate number of samples on which figure for average percentage loss in weight is based.

Note: Where less than 16 samples are taken this is due to rejection of those which included knots or any other defect.

DISCUSSION.

An analysis of the figures taken from the table brings out the following points. Examination of the results from individual sections shows that in general wood taken from near the centre of the heartwood next to the pith is more readily decayed than is that next to the sapwood, which means that there is a progressive increase in resistance to decay from the inner heartwood outwards. The following figures for percentage loss in weight for groups of samples taken from the outermost and innermost heartwood illustrate this.

Section	White rot		Brown rot	
	Adjacent to sapwood	Adjacent to pith	Adjacent to sapwood	Adjacent to pith
1	1.75 (16 samples)	3.38 (16 samples)	1.23 (13 samples)	0.71 (16 samples)
2	1.51 (16 ")	5.06 (16 ")	0.51 (15 ")	8.56 (16 ")
3	1.15 (15 ")	8.93 (13 ")	0.38 (16 ")	11.9 (15 ")
4	1.96 (13 ")	8.78 (13 ")	0.81 (16 ")	22.06 (16 ")
5	2.46 (16 ")	7.73 (13 ")	0.94 (16 ")	21.41 (16 ")
6	4.93 (12 ")	16.84 (8 ")	0.83 (12 ")	5.13 (11 ")

Further, comparing the different sections, there is a significant progressive decrease in resistance to attack from the base upwards for wood taken from the same distance from the sapwood. The only exception to this is in bolt 6 exposed to *Poria incrassata*; this, it is thought, may be due to conditions of moisture in some of the flasks being below optimum.

EXAMINATION OF AMOUNT AND TOXICITY OF WATER-SOLUBLE EXTRACTIVES.

Sowder (7) showed that Western red cedar contains substances soluble in water which are toxic to fungi. These have since been shown by Anderson and Sherrard (1) to be of a phenolic nature. In order to ascertain whether the differences in resistance to decay in various parts of the tree can be correlated to the content of these toxic water-soluble extractives, a series of extractions was carried out on samples adjoining those tested for resistance to decay in each of the six sections. Extracts were obtained from three zones of the heartwood (outer, intermediate, and central) in each of the four lower sections, but from only two zones (outer and inner) in the two top smaller sections. The preparation of the extracts was carried out in the Chemistry Section of the Laboratory and the method used was as follows. Representative samples from each group of specimens were converted to sawdust and the latter thoroughly mixed. Two-gramme samples were refluxed in duplicate with 40 ml. of distilled water at 100° C. for 3 hours. In each case the extract was removed by suction and made up to a volume of 40 ml. with distilled water. The wood residue was washed with 250 ml. of cold water and dried to constant weight at 105° C. Loss in weight due to extraction plus washing was expressed as a percentage of the oven-dry weight of original wood.

The results are given in Table II, from which it will be noted that in every case the percentage content of water-soluble extractives is higher in the outer heartwood adjoining the sapwood than it is in the central heartwood. The figures for the intermediate zone with a few exceptions (as in sections 1 and 4) fall between those for the outer and inner zones.

TABLE II. *Hot water extracts from heartwood*

Sample no.	Hot water extract as per cent. of dry wt.	pH of extract	Sample no.	Hot water extract as per cent. of dry wt.	pH of extract
Section 1: Outer	8.31	4.44	Section 4: Outer	5.94	4.48
Intermed.	4.19	4.71	Intermed.	3.30	4.60
Inner	4.96	4.40	Inner	3.40	4.54
Section 2: Outer	7.33	4.46	Section 5: Outer	4.75	4.54
Intermed.	4.53	4.70			
Inner	3.67	4.72	Inner	3.60	4.64
Section 3: Outer	6.72	4.41	Section 6: Outer	4.19	4.58
Intermed.	3.66	4.71			
Inner	3.19	4.59	Inner	4.0	4.52
Canadian Light	6.89	2.21	..	..	..
Dark	6.86	3.09	..	..	..

The pH of the extracts was determined electrometrically, and it will be seen that it is fairly uniform and not closely linked with the total amounts of extractives. The Canadian material was found to be much more acid than the Scottish, but whether this was due to the relative age of the trees from which the wood was obtained or to some other cause cannot be stated without further investigation. The toxicity of these extracts was examined by means of an agar test in petri dishes, the standard technique used at the Laboratory for testing the toxicity of wood preservatives being employed. Four concentrations of the extracts were used—1, 5, 10, and 15 c.c. of extract being added to 5 c.c. of 8 per cent. malt extract agar, the total volume being made up to 20 c.c. in the first three concentrations with sterile distilled water. Thus the concentration of nutrient remained constant at 2 per cent. of malt. Control plates containing malt agar were included for comparative purposes. The plates were inoculated with *Fomes annosus*, a fungus which is resistant to antiseptics and which is commonly found in this country causing heart rot in *Thuja plicata*. The plates were kept in an incubator at 20° C. and the diameter of the colonies was measured after 7 and 13 days, when growth in the controls had covered the plates. These observations are given in Table III. A scrutiny of these results shows that the addition of the extract brings about a pronounced retardation of growth when 5 c.c. or more of the extract was present, and that this retardation is very much more marked with the extracts prepared from the outer heartwood adjoining the sapwood than with extracts from the central heartwood. This is in close conformity with the results

obtained in the wood sample tests in which it was found that heartwood adjoining the sapwood was the most resistant.

TABLE III. *Toxicity test on aqueous extracts. Growth of Fomes annosus—diameter of colony—cm.*

Sample	Amount of extract in medium							
	5 per cent.		25 per cent.		50 per cent.		75 per cent.	
	7 days	13 days	7 days	13 days	7 days	13 days	7 days	13 days
Section 1: Outer	4.9	10.5	0	+	0	0	0	0
Intermed.	3.0	9.4	2.0	6.6	0.8	4.1	0	0
Inner	4.3	10.0	3.0	9.0	1.4	5.7	0	1.6
Section 2: Outer	4.5	10.5	1.5	5.3	0	0	0	0
Intermed.	4.2	10.3	4.0	10.0	+	4.0	0	0
Inner	3.7	10.0	3.7	9.4	2.7	8.0	1.0	3.3
Section 3: Outer	5.0	11.0	+	3.6	0	0	0	0
Intermed.	4.9	10.7	3.8	9.2	2.9	8.2	1.2	4.5
Inner	3.6	10.0	3.0	8.6	2.8	6.2	+	2.6
Section 4: Outer	4.4	10.5	1.0	5.1	0	0	0	0
Intermed.	3.5	10.0	1.0	4.7	+	2.1	0	0
Inner	3.9	10.0	2.8	8.7	2.8	7.9	1.0	3.6
Section 5: Outer	5.6	11.0	4.0	9.5	0	0	0	0
Inner	4.8	10.6	4.2	10.0	3.5	9.0	1.4	4.8
Section 6: Outer	4.4	10.4	3.5	9.0	2.3	6.9	0	0
Inner	3.2	9.0	3.2	9.4	3.6	8.5	0	1.8
Canadian Light	1.5	3.4	3.2	9.0	0	0	0	0
Dark	+	(Spoilt)	1.5	6.2	0	0	0	0
Controls: no extract	5.2	11.0	..	..	..	..	..	..
in medium	4.9	11.0	..	..	..	..	..	..
	4.9	11.0	..	..	..	..	..	..

The relationship between average percentage loss in weight due to decay in various parts of the trunk and percentage retardation of growth in an agar test, brought about by aqueous extracts from the same heartwood zones, is shown graphically in Fig. 3. It will be noticed that, with one exception, the highest percentage loss in weight of wood due to decay also corresponds with the lowest figure for percentage retardation in growth on malt agar. The one exception is in section 3, where it is apparent that the middle point on the curve is probably incorrect and can, therefore, be ignored. This highest point represents loss in weight due to decay and retardation figure for the innermost heartwood zone. Further, for successive sections from 1 to 6 up the tree, the tendency is apparent for the curves to become less steep, and to shift more and more to the right, indicating a greater difference in resistance to decay within each section between the outer and inner heartwood, and also a progressive decrease in the resistance to decay higher up the trunk. In general the toxicity of the extracts is closely related to the amount of extractives as determined in the analyses. The results are also correlated with the losses in weight sustained by the sample blocks contiguous to those from which the extracts were made.

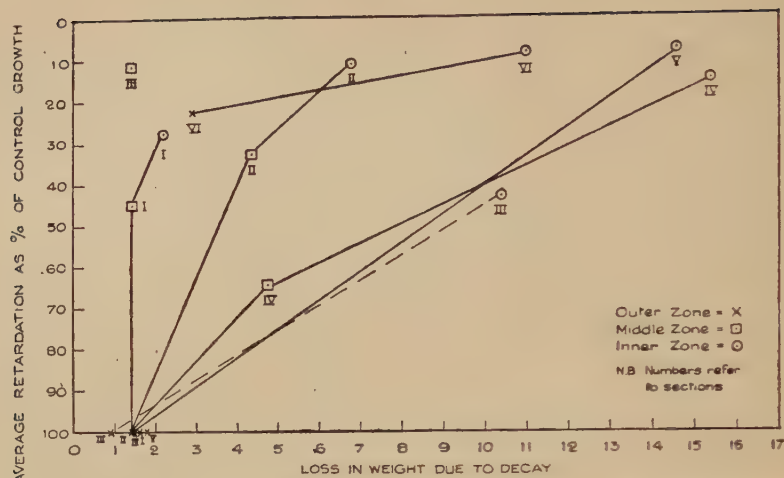


FIG. 3. Relation between average loss in weight per cent. due to decay and per cent. retardation of growth of *Fomes annosus* on malt agar.

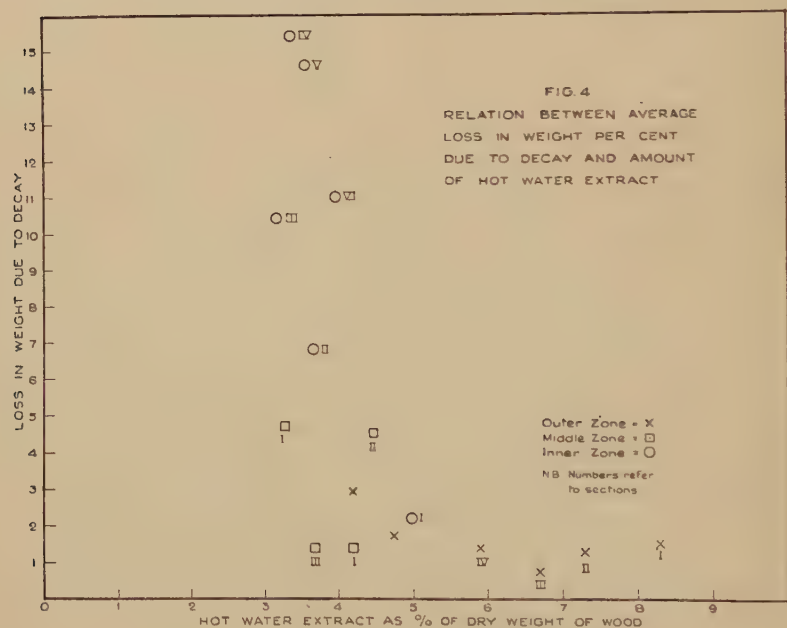


FIG. 4.

This indication that variation in the amount of the toxic material in the hot water extract accounts for the variation in resistance to decay is brought out in Fig. 4. in which figures for percentage loss of weight due to decay¹ for both

¹ The figures for percentage loss in weight of the test samples were taken from Table I for both fungi together, and arranged for the three heartwood zones corresponding to those from which the water extracts were obtained.

fungi from the three zones of heartwood are plotted against figures for percentage of hot water extract from the same three zones for each of the six sections. The distribution of these points brings out again that extracts from the sections taken from the lower parts of the tree are the most toxic, that toxicity of the extract becomes progressively less up the trunk, and, further, that within each bolt the extract from heartwood adjoining the sapwood is more toxic than from the innermost heartwood. The form of distribution follows the normal one obtained from preservative tests; it then abruptly steepens, becoming almost vertical at 4.5 per cent., suggesting that below these concentrations little or no toxic effect is detectable.

It can thus be seen that the results are in general agreement with those obtained by Sherrard and Kurth (6) for *Sequoia sempervirens*.

TABLE IV. *Average loss in weight per cent. of samples after 6 months' exposure, arranged in groups corresponding to samples from which extracts were prepared*

Sample	<i>Polystictus versicolor</i> (white rot)			<i>Poria incrassata</i> (brown rot)			Average of 2 fungi		
	Outer	Intermed.	Inner	Outer	Intermed.	Inner	Outer	Intermed.	Inner
Section 1	1.8	2.2	3.9	1.2	0.6	0.5	1.5	1.4	2.2
" 2	1.5	4.8	5.1	1.1	3.8	8.6	1.3	4.3	6.8
" 3	1.2	2.2	8.9	0.4	1.6	11.9	0.8	1.4	10.4
" 4	2.0	4.5	8.8	0.8	5.0	22.1	1.4	4.7	15.4
" 5	2.5	5.9	7.8	0.9	7.7	21.4	1.7	6.8	14.6
" 6	4.9	..	16.8	0.8	..	(5.1)	2.9	..	11.0
Average for all sections	2.2	3.9	8.5	0.9	3.7	12.9	1.6	3.7	10.1

It is fully realized that the aqueous extracts contain carbohydrates and other substances in addition to the toxic substance, and that without further chemical work it is not possible to specify exactly a minimum content of extractives. Nevertheless the results suggest that, with some reservations, it is possible to obtain a rough measure of the resistance of a given sample of Western red cedar by means of quantitative measurement of percentage hot water extract. Thus samples from which 5 per cent. or more hot water extract is obtained should prove very resistant to decay and, therefore, be suitable for use in all situations where the decay hazard is likely to be high, whereas those from which a lower figure is obtained should only be used for purposes where they will not be exposed to damp. The most toxic extract was that obtained from the outer wood in the section nearest the base of the tree and this wood was found to be the most resistant to decay. It may be calculated that approximately only 0.01 per cent. of the extract from this sample was sufficient to inhibit the growth of *Fomes annosus*; now since the total extract must contain a large proportion of soluble carbohydrates and other substances in addition

to the actively toxic material, this latter substance must be extremely toxic to fungi, as has already been indicated by Anderson and Sherrard (1).

For the sake of comparison, samples of Canadian-grown material were included in the tests; it will be noted that these contained a fairly high concentration of extractives, which are highly toxic and also have a low pH figure. Direct comparison with the home-grown material is not possible, but a somewhat greater resistance of the imported material is indicated, and this is probably connected with the much greater age of the Canadian trees.

ACKNOWLEDGEMENT.

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SUMMARY.

The following conclusions may be drawn from the results of the investigation:

1. The resistance to decay of home-grown Western red cedar wood is of the same order as that of the imported timber.

2. The heartwood from the base of this tree, approximately 65 years old, shows little variation across the trunk in resistance to fungus attack, the timber from this region being very resistant to decay; there is, however, an indication that the outer wood is more resistant to attack by *Polystictus versicolor* than the wood next to the pith. It is probable that this variation would be more marked in a mature tree.

3. The difference in resistance to decay, both by white and by brown rots, between the outer and inner heartwood of each section becomes increasingly marked as one goes up the tree, the most recently formed heartwood being the most resistant, and the resistance decreasing in each case as the centre of the tree is approached.

4. The total average resistance of the timber across the trunk is highest in material taken from the base of the tree, and shows a progressive decrease up the tree. This is true both for white and brown rots, but is shown most clearly with *Poria incrassata* (brown rot), which appears to be more sensitive to variations in resistance.

5. The amount of material soluble in hot water was determined in samples taken from different positions in the trunk and the toxicity of these extracts to *Fomes annosus* was examined. In each of the cross-sections examined it was found that the amount of material extracted by hot water was greater in the outer heartwood adjoining the sapwood than in the central heartwood and that the toxicity of the extracts was correspondingly higher. The resistance to decay of the samples thus appears to be closely correlated with the amount of extractable substances present in them. In the material which was examined serious decay occurred only in wood containing less than 5 per cent. by weight of hot water extractives.

6. Samples of Canadian-grown material were also analysed for extractives and found to contain about 6.9 per cent., a figure exceeded by some of the samples from the outer heartwood near the base of the home-grown tree. The extract from the Canadian material was, however, found to be very much more acid, having a pH of 2.2 as compared with an average figure of about 4.5 in the home-grown.

As these conclusions are based on an immature tree, it cannot be taken for granted that the same would hold good for wood taken from a large mature tree, but it is likely that in the main they would apply, and that wood taken from butt planks of heartwood will be the most resistant to fungus attack, regardless of whether it is from the outer part or from near the centre, but that higher up, planks taken from outer heartwood will be more resistant than those from the centre.

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THE OAK IN SCOTLAND, AND TWO SEMI-NATURAL OAK WOODS IN THE SOUTH-EAST OF SCOTLAND

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INTRODUCTION.

TO many people the woods of Scotland are always associated with the Scots pine. There are many places where the Scots pine is the dominant tree and is also native. Rothiemurchus Forest is, perhaps, the best remaining fragment of Scotland's pine forests. There are still remnants of such forest or wooded areas at Rannoch (Perthshire), in Upper Deeside (Aberdeenshire), and in a few other localities. It may be that the work of Lewis (6) and Samuelson (12) on Scottish peat mosses may have over-emphasized the Scots pine. In many districts the birch is now the dominant tree, as it was when many of the present peat deposits were laid down.

In spite of this, there are still remnants of once extensive oak forests. Perhaps the best is that rare fragment within the grounds of Dalkeith Palace. Small though this area of old oaks may be, it ranks with the New Forest as a lineal descendant of the old native oak forests of Britain. Even within comparatively recent historical times there were considerable areas of oak woods, and there are many references to oak and oak woods, and even forests, in the *First* and *Second Statistical Accounts of Scotland* (14, 15). Interesting information is given about remains of oak-trees and extensive woods or forests by older writers such as Aiton (1) and Steele (16). It is evident that certain names of places indicate the former presence of a wood (e.g. shaw); and much interesting information is given by Watt (21, 22). Another interesting feature in some of the old accounts is the final verification of 'local traditions', handed down through many generations, that woods or forests formerly existed in certain districts. There is both doubt and confusion regarding the use of the word 'forest'. For the most part the word 'forest' in the past was an indication of a hunting area, not necessarily wooded. But the writer feels very doubtful concerning the vegetation covering certain forests or hunting areas before maps or reasonably accurate accounts were available. There are many areas marked forest to-day in maps of Scotland which were wooded in former times, i.e. Ettrick Forest, Yarrow Forest, Jed Forest, &c. The oak remains, dug from many local peat bogs prove conclusively that well-grown, fully developed oaks existed in many parts of Scotland, and also ascended to at least 1,000 feet in certain parts of the Southern Uplands. The disappearance of these ancient oak woods and forests was largely due to the influence of man (3). In many parts of Scotland where peat was not available wood was the only fuel, apart from turf where it could be satisfactorily used. Coal was discovered and

became available too late to save many Scottish woods. Grazing by sheep and other animals prevented natural regeneration and finally exterminated wooded areas. The general distribution of the oak in the past was along the west coast from Dumfries to Glasgow due east to the east coast, and also across to the east coast by a line running approximately from Glasgow to Aberdeen. North of this area in the Central Highlands the pine was the dominant tree, with birch sub-dominant and dominant in places. Oak again occurred round the Moray Firth, in parts of Sutherlandshire, and in parts along the north-west coast. Pine occurred in the higher reaches of the Southern Uplands, often in quantity, but oak certainly grew well at 1,000 feet as peat remains have shown. It is stated in the *First Statistical Account of Scotland* that in Gigha and Cara (Argyll) oak trunks were found in the mosses. A reference is made to oak cutting in Sutherland, that the trees did not afterwards 'spring up', and that there were some old oak woods then in existence. In fact the oak in older times was far more common and widespread than most people realize. Even to-day in Gairloch there are remnants of oak amid large stones or rocks, on a very small scale reminiscent of Wistman's Wood (18). Prostrate, shrub-like, small growths of oak occur, rarely now, on the coast of Kincardineshire and Aberdeenshire. There were often Scots pine and birch-trees also present in some of the oak woods. This mixture of trees and crosses between pedunculate and sessile oaks may be met with to-day in that vague and ill-defined region referred to as the Trossachs. In some parts oak and pine competed with each other (13). The area of the distribution of *Quercus robur* and *Quercus sessiliflora* in Scotland cannot be accurately defined (Fenton, 1938). It would require a very careful and detailed survey before any reasonable and safe conclusion could be reached. It would appear that generally on the heavier soils *Q. robur* occurs, and that *Q. sessiliflora* is confined largely to the lighter and more silicious soils. After the decline of the oak hazel often became (temporarily) the dominant shrub in many parts of Scotland. In the peat in widely scattered parts of Scotland there were plentiful remains of hazel with fully ripened nuts. This suggests a hazel phase in the vegetation succession probably following the oak phase. Unfortunately, most of the peat with hazel remains has been utilized for fuel. Dickie (2) pointed out that the oak occurred in a wild state in various parts of the districts of Aberdeen, Banff, and Kincardine. He also mentions certain coastal parts and the upper region of Aberdeenshire. Trail (19) had in his records that *Quercus sessiliflora* does not occur in a wild state in or near Aberdeen. *Quercus robur* is the oak which is common. In the past huge oaks must have occurred, because Trail refers to the large trunk washed down by the Dee many years ago, indicating that there must have been magnificent oaks at one time in the valley of the Dee. Some years ago two canoes or boats were found in the mud of Loch Kinord (Aberdeenshire), made from the hollowed-out trunks of oaks. There are certainly no oaks approaching that size to-day. Trail (19) also records that 'though the trees flower freely, I have never seen ripe acorns in this part of Scotland, an indication that the tree must have reached its present distribution in Scotland

under more favourable climatic conditions than now prevail'. The writer must correct part of the above statement. Ripe acorns were to be found some years ago on certain trees on the Estate of Durriss (Kincardineshire). Alas, the trees have long since been cut down, but many years ago these ripe acorns were both gathered and examined. Moreover, on rare occasions a few young oaks could be found on Upper Deeside (Aberdeenshire). On certain parts of the Southern Uplands this occurs quite commonly.

There are extraordinary blanks in history as far as it refers to the woods of Scotland. Certainly the region of the Southern Uplands was very poorly wooded long before the North and West of Scotland suffered. A very good account of such isolated facts as are recorded may be found by referring to Richardson (11) and Murray (10). Until comparatively recent times, however, there were some very fine oaks near Hamilton, which could almost rank with those at Dalkeith. Moreover, there may still be found isolated oaks of great age in the country surrounding Glasgow, e.g. near Balfron (Stirlingshire), and in the Strathblane district near Milngavie. Some of the narrower defiles and valleys in the Southern Uplands must have been very inaccessible until comparatively recent times, and therein must have lingered the last remnants of the once extensive 'Forest' of which parts were known as Jed Forest, Ettrick Forest, &c. On some hills there may still be found to-day isolated patches of natural birch, often with heather (*Calluna vulgaris*), but sheep-grazing and burning are rapidly eliminating these few remaining fragments of the old forests.

It seemed desirable that a brief account of the woods at Dalkeith Palace and near Elibank Castle (now in ruins) should be published as examples of what now remains of the old oak forests in the southern parts of Scotland. Some knowledge of these two woods partially supplies the need expressed recently by Tansley (17) when referring to the Southern Uplands of Scotland: 'No information is available about any semi-natural oak woods that may still exist in this very poorly wooded region.'

DALKEITH PALACE OAK WOOD.

Dalkeith Palace has within its policies a considerable extent of woodland. It is with the 'Old' Wood that we are concerned, and it lies east of the Palace. The soil is a medium to heavy loam of a red colour and good depth. There are no records available, but the rainfall, judging by the neighbouring district, would be about 30 inches per annum.

Dalkeith Palace 'Old' Wood though situated in a plain is an outlier of the Southern Uplands of Scotland. The trees are *Quercus robur*, the age of the older trees being about 300 years. This wood had originally been a natural wood, but has been rendered semi-natural within recent historical times by grazing. The area of the old wood consists of a triangular peninsula bounded on two sides by the North and South Esk. There is in places a steep fall of the banks of the two streams, North and South Esk, but elsewhere there are a few small parallel plateaux. The banks towards the north are more shaded

and are in consequence richer in mosses and shade plants. There is considerable variation in the vegetation on the north side of the Esk outside the old wood, but in many parts it would appear that in spite of dense growth in places, apart from one or two isolated patches most of this area is largely artificial and does not fall within the scope of this study. There are outside the old wood two types which are of interest. The first is a small part with oak about 150 years old rather freely spaced with a ground flora of bracken and heather (*Calluna vulgaris*) and some blaeberry (*Vaccinium Myrtillus*). This is a local pocket of vegetation which may be paralleled in many other parts of Britain. If not subjected to interference, this vegetation will probably show little, if any, change with the passing of time. The other interesting part is where a mixture of oak and yew occurs. In places the yew virtually tops the oak, but in others yew is the under canopy. This is probably derived from an old natural vegetation of oak and yew which has been controlled to some extent. In consequence of this and lack of sufficient information and evidence, it would be very unwise to make any further statements, or draw any conclusions. Yew still slowly regenerates in this part, or was still doing so a few years ago. Some beech-trees also occur and struggling through the dead leaves may be found a few young holly-trees. There are some curious and surprising small samples of woodland types within this area.

The ground nearer Dalkeith Palace is in pasture, and an irregular circular space just within the old wood has no trees. This area had probably been cleared of trees (or partly cleared) many years ago. There are several patches of bracken, but it is neither so common nor so frequent as might be expected. Recently (4) an area of $11\frac{1}{2}$ acres was fenced against grazing and rabbits, to provide an opportunity for natural regeneration. This should prove of great interest and value, for many young oaks have already appeared. Unfortunately, access to this has for the present become almost impossible. The oaks at Dalkeith have been known for a long time and have been referred to in the *Statistical Accounts of Scotland* (15, 16). It is there mentioned that they were beginning to show signs of age; probably showing the well-known 'stag-headed' condition of very old trees. This appearance is still the same to-day. As previously mentioned, the oldest trees are over 300 years old. This dates back to 1639 when there is reason to believe there were other fragments of old oak woods still in existence. There are, however, many trees which show not merely two trunks but three, and some of four, while one of five occurs. An examination of some of these strongly suggests the growth of 'saplings' after the trunk had been cut. This was quite normal in many oak woods, although it is evident that coppicing at Dalkeith had never been generally followed. Probably in the past, as to-day, single trees had been cut at long intervals. If this is correct, then the fragment left must go back at least to about A.D. 1300 and most probably much earlier. History records that James IV of Scotland ravaged the forests at Falkland (Fife) for timber to build his navy. We may be quite sure that then, and later, other sources were not forgotten. Doubtless the Dalkeith area was part of the oak forest that lay

below Arthur's Seat all over Priestfield and Duddingston (Edinburgh) where once monks had the right to pasture pigs (pannage).

In one respect the Dalkeith oak wood differs from the New Forest. It has certainly, within recent historical times, been more heavily grazed. Acorns are produced and germinate, but grazing prevents any successful natural regeneration. Hence, although there are plants typical of oak wood, i.e. *Pteridium aquilinum*, *Oxalis Acetosella* and *Brachypodium sylvaticum*, &c., the ground vegetation is grassy, consisting mostly of *Holcus mollis*. There are a few patches of nettles (*Urtica dioica*) but they are not frequent. For the most part the wood is pastured by sheep. Up to 1914 the grazing in the wooded part was by deer. Hence grazing has been an important factor for many years. The inevitable result of this is to restrict the ground flora, and in particular to develop a grassy type. The wood is open, the trees being well spaced, permitting ample light to penetrate between trees. There are a few comparatively young trees (about 100 years), but the majority are very old. There is one small patch of horse-chestnut trees and some hawthorn near the edge of the wood. The vegetation of much of the old woods, where grazing has been general for a long time, varies in different parts, but the following list gives a good impression of the ground flora: *Holcus mollis* (dominant), *Agrostis* spp. (mostly *A. tenuis*) (c), *Festuca ovina* (l), *Deschampsia flexuosa* (c), *Cynosurus cristatus* (o), *Anthoxanthum odoratum* (o), *Arrhenatherum avenaceum* (o), *Avena flavescens* (o), *Dactylis glomerata* (a little), and *Brachypodium sylvaticum* (in clumps) *Potentilla Tormentilla* (o), *Galium saxatile* (c), *Galium verum* (o), *Stellaria Holostea* (l.c.), *Campanula rotundifolia* (l.c.), *Polygala vulgaris* (o), *Calluna vulgaris* (o), *Erica cinerea* (t), *Empetrum nigrum* (t), *Vaccinium Myrtillus* (o), *Luzula maxima* (l.c.), *L. pilosa* (l.c.), *L. campestris* (o), and *Melampyrum pratense* (l.c.).

Mosses identified are: *Hypnum Schreberi*, *Dicranum scoparium*, *Polytrichum commune*, *P. formosum*, *P. juniperinum*, *Mnium hornum*, *Hylocomium squarrosum* (t), *Leucobryum glaucum*, *Plagiothecium undulatum*. The only seedling oaks found growing in the grazing area—with one exception—were where fallen branches had protected the plants against grazing.

The area fenced in 1938 against rabbits and grazing has the following ground vegetation. *Holcus mollis* covers most of the ground, patches of *Pteridium aquilinum*, *Rubus fruticosus*, *Dactylis glomerata*, and *Arrhenatherum avenaceum* occur and a few patches of *Urtica dioica*. Small areas of *Festuca ovina*, *Deschampsia flexuosa*, and *Agrostis tenuis*, occasional tufts of *Aira caespitosa*, *Luzula maxima*, and *L. campestris* are also present. In shady places, *Oxalis Acetosella* is frequent. Other grasses present are *Poa annua*, *P. trivialis*, *Anthoxanthum odoratum*, *Cynosurus cristatus*, *Phleum pratense*, *Festuca pratensis*, and a little *Brachypodium sylvaticum* and *Melica uniflora*. The last two are very local and restricted in the Lothian region. *Rumex obtusifolius*, *crispus*, and *conglomeratus* were found, but are far from common. *Rumex Acetosella* and *R. Acetosella* were common, especially the latter. Other plants present were: *Teucrium Scordonia*, *Digitalis purpurea*, *Hedera Helix*, *Stellaria Holostea*, *Galium saxatile*, *Conopodium denudatum*, *Primula vulgaris*, *Mercurialis*

perennis, *Geranium Robertianum*, *Ranunculus Ficaria*, *Juncus communis*, *Angelica sylvestris*, *Campanula rotundifolia*, *Potentilla Tormentilla*, *Viola Riviana*, *Hieracium Pilosella*, *Ulex europaeus*, *Cytisus scoparius*, and *Lathyrus montanus*. Birch occurs in one part in all stages and is tending to spread, and there are a few plants of hawthorn.

It was very interesting to note that young oaks were found chiefly among the taller vegetation, where there was more moisture and shade. These young trees were frequent in bracken, provided the shade was not too dense, but oaks occurred in about every type of vegetation, occurring on the floor of the wood. In one section, no less than 6 two-year-olds were recorded.

The mosses recorded were: *Polytrichum commune*, *P. juniperinum*, *P. formosum*, *Hylocomium squarrosum*, *H. loreum*, *H. splendens*, *Plagiothecium undulatum*, *Dicranum scoparium*, *Hypnum cupressiforme*, *H. cuspidatum*, *H. Schreberi*, *Campylopus flexuosus*, *Fumaria hygrometrica*, *Bryum* spp., *Brachythecium purum*, *Thuidium tamariscinum* (t).

ELIBANK CASTLE OAK WOOD

Elibank Castle Wood lies just west of the ruins of Elibank Castle. It is quite different to Dalkeith Wood, since the trees are mostly crosses with distinct leanings towards *Quercus sessiliflora*. A few trees of *Quercus sessiliflora* occur; situated in the Tweed Valley on the northern base of a hill dipping gently towards the Tweed. Excluding a patch of obviously planted conifers on the eastern side, the total area is $1\frac{1}{4}$ miles long by $\frac{1}{4}$ mile in depth. No detailed study of soil has been made, but it is of a silicious nature and in places rather shallow. Owing to the northern-facing aspect of this wood there would be very little sunshine during the winter months. The rainfall is about 40 inches per annum.

In the Peebles area of the Tweed valley and neighbouring valleys isolated oak-trees of good age occur. Acorns are produced and young seedlings may be found often far from the nearest tree. Very few of these survive, for almost the whole area is used for sheep-grazing, so that grazing pressure and heather-burning prevent any natural regeneration. In the policies (equivalent to English park land) of some of the older country houses, old oak-trees still survive. Some of these are undoubtedly lineal descendants of the old forests. As the grassland in which these oaks grow is in constant use for grazing, no young oaks can survive to replace the older trees, so that they have been slowly but steadily dying out for many years. Hence an oak wood is of comparatively rare occurrence in the region of the Southern Uplands. The oak wood near the ruins of Elibank Castle is thus of peculiar interest, not merely on this account, but also because it is a wood of crosses of pedunculate and sessile oaks, and *Quercus sessiliflora*. The flora of the woods near Elibank Castle consisted (apart from oaks) of some birch scattered through a small part of the wood, a few *Pyrus Aucuparia* and many seedlings, and a few *Sambucus Ebulus* near the edge of the wood. *Scilla non-scripta* and *Anemone nemorosa* occur locally. *Lonicera Periclymenum* is present, but not abundant. There are patches of *Pteridium*

aquilinum (c) and *Polypodium Dryopteris* (l.c.) and a small clump of *Urtica dioica*. The most common grass is *Holcus mollis* (a) but *Agrostis* (chiefly *A. tenuis*), *Festuca ovina*, and *Deschampsia flexuosa* are common. The other plants present are *Digitalis purpurea* (l), *Mercurialis perennis* (o), *Galium saxatile* (c), *Viola Riviana* (l.c.), *Scabiosa succisa* (o), *Luzula maxima* (l.c.), *L. pilosa* (l.c.), *L. campestris* (o), *Teucrium Scorodonia* (l.c.), *Vaccinium Myrtillus* (o), *Calluna vulgaris* (o), *Ajuga reptans* (o), *Primula vulgaris* (o), *Oxalis Acetosella* (c), *Lysimachia nemorum* (l), and *Rhinanthus Crista-galli* (o).

The mosses identified were: *Hylocomium loreum* (c), *H. triquetrum* (l), *H. squarrosum* (l.c.), *Dicranum scoparium* (c), *Hypnum cuspidatum* (f.c.), *Climacium dendroides* (v), *Hypnum Schreberi* (c), *Minium hornum* (l.a.), *Plagiothecium undulatum* (l.c.), *Brachythecium purum* (l), *Polytrichum commune* (l.c.), and *Spagnum* spp. (l). The following lichens were found: *Evernia prunastri* (o), *E. divaricata* (o), *Cladonia pyxidata* (o), *C. foliacea* (o), *C. rangiferina* (l.c.)? and *Peltigera canina* (l).

An interesting patch in the wood was almost dominated by a rather open growth of *Pteridium aquilinum*. There was also a dense growth of *Polypodium Dryopteris* and patches of *Aspidium Filix-mas* and *A. spinulosum*. Most interesting of all, a few oak seedlings occurred in a patch of *Pteridium aquilinum* and *Polypodium Dryopteris*. This was the only part of the wood where any oak seedlings were found except two isolated specimens near the edge of the wood. This is the second occasion in Scotland that young oaks (seedlings or otherwise) have been noted growing well, while mixed with tall-growing herbage. In the fenced part of Dalkeith Woods, the young oaks seem to be growing well, even when in a rather shaded position. It was also noticed that there was little, if any, difference, whether the vegetation was grassy or even bracken, or gave protection by shade or provided moisture. This has also been observed in certain parts of England. Unless the writer is mistaken, this also occurs in certain parts of New Forest. One might almost conclude from this that too much interference with Nature is not a good thing in the natural regeneration of young oaks. One of the most successful growths of young oak the writer has seen, was in a waste piece of ground in Hampshire where young oaks were successfully growing through a dense growth of gorse (*Ulex europaeus*) and young rowan-trees (*Pyrus Aucuparia*).

In the Elibank Castle Wood the trees (at times) produce a very good crop of acorns (e.g. 1939), yet few young oaks can be found. In the autumn of 1939 only a few could be found, and these were all one year old. In 1940 not a single acorn could be found, and very few oak seedlings. Several oak seedlings were found during the summer of 1941. No young oaks could be located in spite of a careful search. There are insufficient rabbits to cause the loss of these young trees, and sheep are not pastured in the wood, nor are there any traces of cattle or horses. There remains the question of destruction by mice and voles, and until definite information is available to the contrary, it must be assumed that these may be the cause of the failure of natural regeneration (Watt, 20). It is a very rare occurrence to find young oaks in this district.

Destruction of oaks by field-mice was recorded by the Earl of Haddington over two centuries ago (5). A few young oaks occur mixed with birch on the hill-side just above the boundary wall of the wood.

DISCUSSION

It is quite unnecessary to make detailed comparisons with the lists of plants of typical oak woods given in Tansley's *The Vegetation of the British Isles* (17), where reference to various authors may also be obtained. There is obvious similarity between many of the examples quoted by Tansley and both the Dalkeith Oak Wood and that near Elibank Castle. The latter wood comes very near the type at Craigendarroch, Ballater, Aberdeenshire (9, 17), which in the past was coppiced. The old wood in Dalkeith Palace Grounds belongs to group 2 of Tansley's (18) *Natural and Semi-Natural British Woods*. The shrub layer was destroyed long ago by grazing. The vegetation of the surface or ground layer has also been greatly modified till it is now mostly a grassy type dominated by *Holcus mollis*. There are some suggestions of group (4) 'Facies of dryer and more acrid soils', but this is entirely a secondary effect due to the grazing influence producing a pasture-like type of ground vegetation.

The Elibank Castle Oak Wood falls under group (5)—heathy oak wood, a type which must have been very common in many parts of Scotland in past times. A comparison of the vegetation shows very strong similarities. It is evident that for some time now Elibank Castle Wood has been left to go its own way, and may therefore be considered semi-natural. Beyond a few trees recently felled, there is no sign of any real disturbance. It is unfenced and intersected by a very second-rate road. The proximity of a private house also doubtless assists in maintaining this wood under almost natural conditions. It is on the south side of the Tweed and not too readily accessible from the Peebles-Galashiels road.

Other small areas of oaks may be found in isolated parts of Scotland. For instance, one such wood occurs two miles west of Elgin. Some of the oaks are of good size. They represent all that now remains of an extensively wooded area, which once occupied much of the southern shore and level lands of the Moray Firth. This wood might once have been considered semi-natural, but in the past it has been much altered, and changes are still occurring.

Oaks occur in Roslin Glen (near Edinburgh), mostly on the north side. They are hybrids and *Q. sessiliflora* but some come very near *Q. robur*. There are small pockets of oak in this finely wooded, steep-faced valley which are natural or semi-natural, and but for rabbits, &c., natural regeneration might occur in places. Many of these oaks, as well as other trees, are growing in situations where they could not have been planted. For the most part the oaks are small, some almost stunted, for in places rock is very near the surface. There is *Vaccinium Myrtillus* near the oaks and a remarkable, rich ground flora in parts of the Glen. A walk through the Glen reveals a flora more in keeping with certain parts of England than with Scotland. Quite a number

of rare plants of the Lothians are found in or near Roslin Glen. None of the trees are very large, but one which had been cut some years ago on the edge of a precipice was nearly 200 years old. One, more recently cut, of a more reasonable size, was nearing the double century. Actually, most of the trees are older than they seem, as not a few are stunted, a fact reflected even in the size of the leaves. The *Field-Club Flora of the Lothians* (8) (1st ed. 1927) records *Q. sessiliflora* as rare and *Q. robur* as frequent. In the later edition (1934) this is omitted. The oaks in Roslin Glen, like those at Dalkeith, are attacked by the Beef-steak fungus (*Fistulina hepatica*).

Old records indicate that Duddingston, south of Arthur's Seat, Edinburgh, was formerly covered by oaks. It is highly probable that this area linked up with the oaks at Dalkeith, and that this wood stretched beyond Roslin Glen and covered much of the Penicuik valley between the Moorfoot and Pentland Hills. Hazel still occurs in Roslin Glen, and its remains have been found in peat in the Penicuik valley. Only last autumn birch (*in situ*) and bark of Scots pine were found in a peat cutting in Boghall Glen (Pentland Hills). Hence it would appear that much of the valley, and even side valleys, were once wooded areas.

There are those who attribute the passing of the oak to a change in climate. This question is very controversial, and one that is almost impossible to answer in a convincing manner. There has, however, within recent time been a slight but definite change in the climate (7), and some of the older writers may yet be proved to be correct (1, 16). Nevertheless, the semi-natural oak woods of any consequence to-day are mostly in small isolated patches in very inaccessible parts, or like Dalkeith, an area isolated and protected from the general destruction of mankind. Natural regeneration has been suppressed not merely by cutting down and destroying trees, but by the long continued grazing by sheep and other animals. The present treeless condition of the Southern Uplands of Scotland is, therefore, the natural and inevitable result of centuries of destruction, spoliation, and neglect.

SUMMARY

Formerly there were extensive oak forests in Scotland. Both *Quercus robur* and *Quercus sessiliflora* were common. A considerable part of the Southern Uplands was formerly the home of the oak, especially the valleys up to the 1,000-foot level. One example of a pedunculate and one of a mixed oak wood are described. Both woods are semi-natural and afford interesting comparisons with oak woods elsewhere. The chief agency, both direct and indirect, in forest destruction in the Southern Uplands has been man. To-day only a few small, isolated examples survive which can be considered lineal descendants of the old Scottish oak forests.

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NOTE—Since this paper was submitted, the author has found that the wood called Eli-bank Castle Wood is marked on Blau's Map of 1650-1660. As the position and extent are in agreement with present maps, it is evident that a wood has occupied this site from some period previous to 1650 to the present time. This provides still further evidence that the wood may be classified as semi-natural.

5th December, 1941.

SOCIETY'S AND OTHER NEWS

WAR-TIME ARRANGEMENTS

WAR work and transport difficulties have made the holding of Annual General Meetings impracticable, and, as the position will probably remain the same throughout the war, the Council decided to circularize the members of the Society and ask for the consent of the Professional Members (who alone have voting rights) to proposals (1) for suspending temporarily those parts of the Constitution and Rules which require the election of Office-bearers and Councillors each year and the holding of Annual Meetings; (2) for confirming the election of the Office-bearers and Councillors due to take office on 1 January 1940; (3) for continuing all Office-bearers and Councillors in office during the temporary suspension of the Constitution; and (4) for empowering the Council to manage all the affairs of the Society, including the filling of casual vacancies in its ranks and the appointment of Hon. Fellows and Investment Trustees, during the suspension.

The circular letter to the above effect, dated 19 March 1941, was duly issued along with a form of Assent to the proposals, and over two-thirds of the Professional Members have now signed and returned the Assent. The Council is accordingly managing the affairs of the Society on this temporary basis.

OBITUARY

The Late Sir Hugh Murray

THE late Sir Hugh Murray was one of the last, if not the last, of the members of the Indian Forest Service who received their technical training at Nancy. He went out to India in 1882 and until 1934—fifty-two years—was actively engaged in forestry in India and in Great Britain. His death took place at Bodenham near Salisbury on 9 February 1941.

The son of Lieutenant-Colonel Charles Murray, 42nd Royal Highlanders, he was born on 27 April 1861 and educated at Trent College. In India his service was spent in the Bombay Presidency, where he rose to be Senior Conservator of Forests and an additional Member of the Provincial Legislature. Had he remained in India it is probable that he would have been appointed Inspector-General of Forests, but he retired in 1911 to live in England.

At the outbreak of the Great War Murray was employed on staff work at the War Office but passed on to the Timber Supply Department, where in due course he was appointed Deputy Controller.

At the end of the war he came to the newly established Forestry Commission as Assistant Commissioner for England and Wales and until 1924 held that position, in which he was succeeded by the late H. A. Pritchard. From 1924 to 1934 Murray was a member of the Commission and attended the monthly meetings with the greatest regularity. He was a fellow of this Society from its formation.

In the course of his long career Murray made many friends and acquired much wisdom which he was always ready to bring to bear on a knotty problem. He did not set up to be a great technician, though his long experience of forests might have entitled him to do so. He preferred rather to draw out the technical knowledge of his

assistants and to apply to it the test of common sense. His best work for the Forestry Commission was in the acquisition of land for the new State Forests. His methods and ideas on values were unorthodox but none the less successful in securing large areas at low rates. Next in importance was his good influence on the young members of the new Service who looked to him for help and guidance. He was a good companion with a fine sense of humour and a strong interest in human problems.

In recognition of his services in India Murray was given a C.I.E., for his work in the Great War a C.B.E., and was knighted after his appointment as Forestry Commissioner.

He married first Gwendoline Mabel Langridge and had two sons. Secondly he married Dorothy Christine, daughter of the late Right Hon. Sir William Mather, and had two sons and a daughter, and is survived by Lady Murray, one son and one daughter.

R. L. R.

REVIEWS

Manual of Cultivated Trees and Shrubs. By ALFRED REHDER, Associate Professor of Dendrology and Curator of the Herbarium, Harvard University. 2nd Edition, pp. i-xxx, 1-996, with Map of Climatic Zones. The Macmillan Company, New York: Macmillan & Co. Ltd., London. 1940. 42s. net.

Review by W. DALLIMORE

SINCE the publication of the first edition of this work in 1927 it has been looked upon as one of the most reliable botanical reference books on hardy trees and shrubs, but during the intervening years there have been so many new introductions, and the International Rules governing botanical nomenclature have been so amended that a thorough revision of the work became necessary, and the result is the present volume.

On opening the book attention is attracted by the frontispiece, a map of North America divided into seven climatic zones, from No. 1 which embraces Arctic regions to No. 7 which takes in the subtropical or almost tropical southern States. In the descriptions of plants appearing later in the work, the degree of hardiness of each one is indicated by reference to the appropriate zone. Following a short preface there is an introduction of several pages which indicates the chief features of the work. Then a number of pages are devoted to abbreviations of references to illustrations, followed by an explanation of the abbreviations of signs used in the descriptions. A synopsis of the orders and families contained in the book is followed by an analytical key to the families and aberrant genera treated in the work, then 902 pages of descriptions of plants are succeeded by a glossary of botanical terms used, and the work is completed by an excellent index extending to 76 pages.

An idea of the scope of the work may be gathered from figures given in the introduction. The author states that 'The trees, shrubs, and vines described in this book belong to 486 genera distributed among 113 families. The number of species, including a small number of horticulturally important hybrids, fully described and represented in the keys is about 2,535, with about 2,685 varieties. Besides these there are about 25 genera, 1,400 species and 540 hybrids briefly described or mentioned and appended to the families, genera, or species to which they are most closely related, or in the case of hybrids, to one of the parents.'

In arrangement the sequence followed is chiefly that by Engler and Prantl in their *Natürliche Pflanzenfamilien* and in Engler's *Syllabus*.

In the descriptions, a key to the genera in each family is given, and further keys are given to the species in all the larger genera. These keys will be found to be very useful by those who have to work out the identity of species. Specific descriptions include the approximate height in metres, habit, condition of branchlets, leaves, flowers, fruit, references to illustrations in other works, the most important synonyms, native country, date of introduction, with, when necessary, the most important varieties.

The observance of the International Rules relating to botanical nomenclature has made the substitution of obscure specific names for better-known ones essential in some cases, while in a few instances botanical limitations placed upon genera or species have been responsible for certain name changes. However, Professor Rehder's world-wide reputation for careful work leaves no doubt about the accuracy of his decisions. A few noticeable alterations of names are *Pinus Griffithii* instead of *P. excelsa* or the later-used *P. Wallichii* for the Bhutan Pine, *Quercus hispanica* var. *Lucombeana* instead of *Q. Lucombeana* for the Lucombe Oak, *Quercus petraea* instead of *Q. sessiliflora* for the Durmast Oak, *Ulmus carpinifolia* takes the place of *U. nitens* for the smooth-leaved Elm, the Cornish Elm is reduced from specific rank to that of variety *cornubiensis* of *U. carpinifolia*, the well-known *Magnolia stellata* becomes *M. Sieboldii*, the common *Hydrangea* so well known as *H. Hortensia* is correctly *H. macrophylla*, and the tree that many of us have known for more than half a century under the name of *Sequoia gigantea* is described in the present work as *Sequoiadendron giganteum*. Cultivators of the Cricket-bat Willow will find that the well-known name of *Salix coerulea* has given place to *S. alba* var. *calva*. However, we shall get used to the changes just as we have done to the use of *Picea Abies* instead of *P. excelsa* for the Common Spruce, *Larix decidua* instead of *L. europaea* for the European Larch, and *Pseudotsuga taxifolia* instead of *P. Douglasii* for the Douglas Fir, changes which also became necessary through the observance of the International Rules governing botanical Nomenclature.

Commercial Timbers of the United States: their structure, identification, properties and uses. By H. P. BROWN and A. J. PANSHIN. pp. xxxi+554, with 75 text-figs. and 312 photomicrographs. McGraw Hill Publishing Co. Ltd., London. 1940. Price 35s.

Review by S. H. CLARKE

THIS book is a replacement of an earlier volume entitled *The Identification of the Commercial Timbers of the United States* by the same authors; it is enlarged to more than twice the size of the earlier book by the introduction of sections devoted to a picture of the tree in the plant world, an outline of the growth of timber, and intimate descriptions of macroscopic and microscopic structure. A chapter headed 'Miscellaneous Information about Wood' and occupying some 80 pages, deals with such subjects as grain, figure, and defects (including those due to seasoning and decay).

The latter half of the book is devoted to identification, and is a revised edition of the earlier work. There are macroscopic and microscopic keys, and detailed descriptions of the principal timbers of the United States. Some of the descriptions have been revised, and the value of all has been greatly increased by the addition of notes on uses, references to literature, and to diagnostic features of special importance in separating timbers likely to be confused. The photomicrographs are all of excellent quality and those illustrating types of vessel pitting call for special praise. The publishers have maintained their usual high standard in reproduction.

Readers of this journal will no doubt wish to know whether in the opinion of the reviewer this book fills the proverbial 'long-felt want'. In so far as the 'want' is that of students of a particular school it would be presumptuous to offer an opinion. Having regard to the development of general text-books on wood during the last ten years, however, it is possible to make some estimate. Although the book refers to the properties of timber, the authors appear to have been more than a little preoccupied with the subject of identification. The accounts of anatomical structure are written mainly with this in view, and although the 'Miscellaneous' chapter contains a great amount of valuable information it may be considered disproportionately small by engineers and architects to whom the authors refer in their preface. The subject of tension wood is dismissed with the sentence 'Little information is available relative to the structure and properties of tension wood except that in some tree species, it is characterised by the presence of large numbers of gelatinous fibres'. In fact, quite important discoveries have been made during the last five years and some of the most notable (e.g. the work of Jacob, see review in *Forestry*, vol. 13 (1) p. 68) should have been mentioned.

The claim that this is a 'well-rounded text book' may be questioned on the ground that the treatment of the properties is inadequate; on the other hand, students will find it a valuable introduction to the description of timbers, and the revised second part will be extremely valuable to all who are interested in American timbers. In the interests of economy, however, the two parts might well have been published separately.

Drying Rates of Blue-stained and Bright Lumber. By T. C. SCHEFFER, *Southern Lumberman*, 162 (2039): 46-48. 15 March 1941.

FROM controlled experiments involving uniform drying conditions and short sections of one-inch by six-inch unseasoned lumber of loblolly pine and sweet gum it was concluded that blue stain does not retard drying but in various degrees promotes it. Equilibrium moisture contents of stained and bright wood were practically the same. Occasional reports that shipments of lumber with a substantial amount of stain tend to be heavier than similar lots containing bright material are believed to be based on observations of stock that had not been comparably seasoned.

Decimal Hoppus Tables: Showing the Solid Contents of Round Timber in Hoppus Feet and Decimals. By S. E. WILSON, M.SC., PH.D., D.I.C., Scientific Computing Service, Ltd., London. 1941. Price 6s.

THIS book appears at an opportune time when measurement of timber is being done on such a large scale. The orthodox Hoppus tables have always appeared unwieldy to those accustomed to decimals, and many used tables of their own compiling in feet and decimals of feet. It is certain, therefore, that this book will have a wide appeal, and to Dr. Wilson thanks are due for undertaking the task of compiling it.

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THE Council has decided for reasons of economy in paper, &c., that *Forestry*, Volume XV, 1941, shall consist of one Number only.